

PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

150th Session (1937-8)

Part 4

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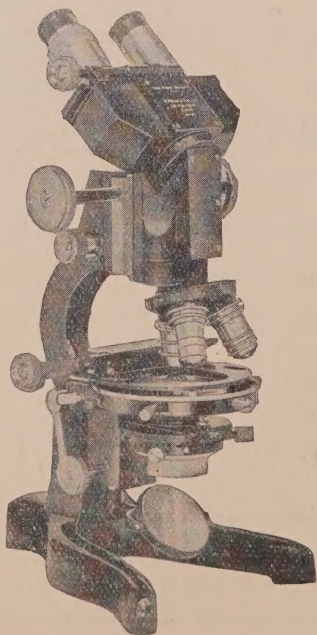
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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

150th Session (1937-8)

Part 4

PROCEEDINGS OF THE 150TH ANNIVERSARY CELEBRATIONS, 24-26 MAY 1938

The Society met in open session at 3.0 p.m. on 24 May in the lecture theatre of The Royal Institution of Great Britain, 21 Albemarle Street.

Mr. J. RAMSBOTTOM, O.B.E., Dr.Sc., President,
in the Chair

The PRESIDENT read and despatched the following telegram, expressing the Society's loyal greetings to **His Majesty The King** on the present occasion :—

The President, Council, and Fellows of the Linnean Society assembled in General Meeting on the occasion of the 150th Anniversary of the Foundation of the Society tender to His Majesty the King their Patron an expression of their Loyal Greetings and Humble Duty

(Signed) RAMSBOTTOM, PRESIDENT.

The PRESIDENT read the following letter from the Treasurer to **Her Majesty The Queen** :—

BUCKINGHAM PALACE.
6th May 1938.

The President,
Linnean Society of London,
Burlington House,
London, W. 1.

Dear Sir,

I have submitted your letter of 28th April, addressed to Captain Streatfeild, to The Queen, and Her Majesty has graciously expressed a wish to belong to The Linnean Society of London, which she was interested to learn celebrates the 150th Anniversary of its foundation on the 24th May next.

Yours faithfully,

(Signed) B. V. BROOKE,
Treasurer to Her Majesty The Queen.

The intimation that Her Majesty had graciously consented to become an Honorary Member was received with acclamation.

Although unexpected, Addresses and messages of Congratulation were received from the following ; in some instances being handed to the President by Delegates present :—

Argentine—

Sociedad Argentina Ciencias, Buenos Aires.

Belgium—

Académie Royale de Belgique, Bruxelles.

Société Royale Linnéenne et de Flore, Bruxelles.

Société Royale Zoologique de Belgique, Bruxelles.

British Isles—

The Malacological Society of London.

Society for the Promotion of Nature Reserves.

The Conchological Society of Great Britain.

Marine Biological Association of the United Kingdom.

Royal Philosophical Society of Glasgow.

National Museum of Wales, Cardiff.

Ashmolean Museum and Museum of History of Science,
Oxford.

Quekett Microscopical Club.

Cardiff Naturalists' Society.

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British Empire Overseas—

Linnean Society of New South Wales, Sydney.

National Museum of Canada, Ottawa.

Royal Botanic Garden, Calcutta.

Czecho-Slovakia—

Czech Academy of Sciences and Arts, Prague.

Denmark—

Dansk Botanisk Forening, Copenhagen.

Finland—

Societas pro Fauna et Flora Fennica, Helsingfors.

France—

Académie des Sciences de l'Institut de France.

Muséum National d'Histoire Naturelle, Paris.

Société Linnéenne de Normandie, Caen.

Germany—

Deutsche Zoologische Gesellschaft, Berlin.

Zoologisch-Botanische Gesellschaft, Wien.

Botanisches Institut und Botanischer Garten der Universität,
Wien.

Italy—

Società Botanica Italiana, Firenze.

Netherlands—

Koninklijke Akademie van Wetenschappen, Amsterdam.

Norway—

Botanical Garden and Museum of the University of Oslo.

Portugal—

Sociedade Broteriana, Coimbra.

Sweden—

Svenska Linné-Sällskapet, Uppsala.

Kungl. Universitetet i Uppsala.

Naturhistoriska Riksmuseum, Stockholm.

Kungl. Svenska Vetenskapsakademien, Stockholm.

Regia Societas Scientiarum et Litterarum Gotoburgensis.

Hortus Botanicus Gotoburgensis.

Hortus Botanicus Upsaliensis.

Professor Einar Lönnberg, F.M.L.S., Stockholm.

Switzerland—

Musée d'Histoire Naturelle, Bâle.

Professor Gustav Senn, F.M.L.S., Bâle.

U.S.S.R.

Society of Naturalists of Moscow.

United States of America—

The Academy of Natural Sciences of Philadelphia.

The American Society of Zoologists.

New England Zoological Club, Harvard College.

New York Zoological Society.

The Linnaean Society of New York.

The PRESIDENT addressed the Meeting as follows :—

PRESIDENTIAL ADDRESS.

By J. RAMSBOTTOM, O.B.E., M.A., DR.SC.

LINNAEUS AND THE SPECIES CONCEPT.

It is my pleasure to thank the Fellows of the Linnean Society of London for the high honour they conferred on me by electing me as their President. It is my privilege on their behalf to welcome our many guests from this country and overseas, to thank them for their presence, and to express the hope that they will find both pleasure and profit in our company and that same delight in London which led the illustrious Linnaeus, after his visit in 1736, to describe it as *Punctum saliens in vitello orbis*.

A few words of explanation seem called for about to-day's arrangements. According to our Charter it is necessary for the Fellows of the Society "to assemble together at their last or other usual place of meeting" on May 24th to carry out the election of Council and Officers, and, according to our Bye-laws the Meeting has to begin at 5 o'clock. In these circumstances we have arranged to carry out here those parts of the meeting not affected by the Charter, and for our Fellows to proceed afterwards to Burlington House, to fulfil our Statutory obligations.

The date May 24th was chosen for our Anniversary Meeting because it was thought to be Linnaeus's birthday, it being overlooked at the time of the Charter, 1802, that May 13th in the Swedish Calendar of 1707 did not correspond to the same date in the Russian Calendar, but that there was a day's difference : the date should be May 23rd.

Fifty years ago to signalize the centenary of the Society it was decided to institute a medal, to be known as the Linnean Medal, and to be presented on each anniversary to one of the most illustrious biologists as an expression of the Society's estimate of his services to Science. It is of some interest in view of the subjects we are to discuss that two medals were awarded at the Centenary meeting, one to Sir Joseph D. Hooker, the other to Sir Richard Owen. Since then it has been customary for botanist and zoologist to alternate. This year, as you know, the Council's choice is Sir D'Arcy Wentworth Thompson, and I would ask him to come forward to receive his medal.

Sir D'ARCY.—

Since its foundation, the Linnean Society, while maintaining the traditions associated with the great Swedish naturalist whose name it bears, has always welcomed to its fellowship the disciples of the newer schools whose studies of the organic

world have led them into fields of knowledge Linnaeus never knew. It seemed to our Council, therefore, especially fitting that on this, our one hundred and fiftieth anniversary meeting, the highest honour in our gift should be conferred on a naturalist who, more than any other of our time, has shown himself to be at home in both the fields of the old and of the newer learning.

The founders of our Society were, most of them, classical scholars as well as men of science, and we can well imagine Bishop Goodenough and Sir James E. Smith exchanging snuff-boxes while they discussed and approved the ripe scholarship of your 'Glossary of Greek Birds' and your translation of Aristotle's 'Historia Animalium'. But, if these works are in the eighteenth century tradition, your 'Growth and Form' is no less distinctively in that of the twentieth. Published in war time, it was one of the first scientific books some of us read when we came back to civil and scientific life in 1919. It is already something of a classic on the shelves of the younger biologists of the experimental school, and we turn to it again and again not only for information, but for inspiration and delight.

In selecting you, Sir, as the recipient of the Linnean Medal, we have no doubt that our choice is one that would have pleased Linnaeus himself.

In giving an Address on an occasion such as this it might have been appropriate to have said a good deal about the history of our Society. Fortunately this is unnecessary, as within the last fortnight 'A History of the Linnean Society of London' has been published. This was written by Lt.-Col. A. T. Gage, who was Librarian and Assistant Secretary of the Society from 1924 to 1929, and all Fellows of the Society would wish to express to him their thanks for his continuing the writing of the volume after his retirement and during a period of severe bodily illness.

One hundred and fifty years does not seem a very long period when viewed in the light of the humanities, but in science the changes have been so many and so great that a scientific society which has consistently followed its aims for that period may perhaps claim to be somewhat venerable. Whether this is so or not, the year of our birth saw the founding of Australia, the constitution of the United States of America, and the appearance of 'The Times'.

It has been arranged that the Presidential Address shall serve as an introduction to the two symposia which are to be the special feature of our celebrations—'The concept of species from the time of Linnaeus to the present day' and 'Geographical isolation as a factor in species formation'.

No name is more closely associated with the concept of

species than that of Linnaeus. In trying to estimate his influence on the thought of his contemporaries and of his successors we must have regard to his predecessors. Linnaeus himself certainly studied the writings of those who preceded him; indeed, one of his earliest works was his 'Bibliotheca Botanica' (1736) which contains over 1000 titles. From his publications, from the marginal notes in the books of his library, and from his correspondence it is evident that he made full use of any fact or idea which was suitable for his purpose. When studying the writings of Linnaeus, as indeed of all men of his eminence, there are certain points that have to be borne in mind. It is necessary to consider what was the main purpose of his work, and thereon to judge whether or not he succeeded. Incidental general observations on theoretical subjects must be interpreted by their relations to particular problems. It must not be assumed that his opinions remained fixed throughout his career—that is, from his first book in 1735 till his last in 1771, and one must guard against reading into some odd sentence the germ of a theory which was formulated at a later date.

Since the theory of evolution gained general acceptance following Darwin's 'The Origin of Species', it has often been pointed out that the idea of transformism can be traced in classical writings. Moreover, many Fathers of the Christian church did not accept the Mosaic account of the Creation as necessarily containing scientific as opposed to moral and spiritual truth. As more and more became known of the animal world and of the vast numbers of smaller organisms, the limit of Adam's capacity to name every living creature, and of the ark's capacity to hold them, apart from the inability of vegetation to withstand prolonged submergence, led many to postulate subsidiary creations, and spontaneous generation from mud and slime. Transformism as a theory was readily accepted both by theologians and naturalists. It is not necessary to follow any of these or later controversies; they were often marked by acute reasoning and often lit up with humour, particularly as new lands were discovered. The impression I have gained is that the Fathers of the Church, meeting with difficulties of biblical interpretation, discussed philosophically the account of the Creation. Then followed a period when philosophy was replaced to some extent by assertion. At the Reformation, Luther threw his weight in favour of the literal acceptance of the Scriptures, rejecting the allegorical and mystical interpretations of the earlier theologians.

When considering Linnaeus's view on species we have to remember his period and his religious connections. He came from a religious stock and would probably have been a Lutheran

minister if he had proved amenable to the necessary educational requirements. He himself was devout and orthodox, and readily accepted the authority of the Church. Even so, his works were banned in the Papal States from 1758 till 1773 * either because of the supposed immorality of his teaching concerning the sexuality of plants † or because he had arranged animals in a way different from Moses—or both. Moreover, one of Sweden's foremost Lutheran prelates, Bishop Svedberg, described his explanation of the reddening of water by myriads of minute insects as "a Satanic abyss", but Linnaeus in a letter to Eloius shields himself by saying "it is certainly a miracle that so many millions of creatures can be suddenly propagated . . . it shows undoubtedly the all-wise power of the Infinite" ‡—a clear indication of his attitude to these matters. Whatever the underlying motive, Linnaeus did not wish to raise any controversial point about religion. This is seen clearly in a letter to Gmelin in 1747. Linnaeus in his 'Systema Naturae', 1735 (of which Gmelin had probably seen the recent German seventh edition), had placed man as a genus of Anthropomorpha in the Quadrapeds as *Homo*, with the description, "nosce te ipsum."—together with *Simia* and *Bradypus*.

The letter runs:—

"You disapprove of my having located Man among the Anthropomorphi §. But man knows himself. Now we may, perhaps, give up those words. It matters little to me what

* "The Pope, who fifteen years ago ordered those of my works that should be imported into his dominions to be burnt, has dismissed the professor of botany, who did not understand my system, and put another in his place, who is to give public lectures according to my method and theory." Letter from Linnaeus to C. Thunberg (see J. Trapp's Translation of D. H. Stoeber, 'Leben des Ritters C. von Linné', p. xii; 1794).

† Linnaeus had stated that in the animal as well as in the vegetable kingdom there were frequently several males to one female (plures mariti; una foemina in eodem thalamo). Perhaps the strongest opposition to this view came from J. G. Siegesbeck, Professor of Botany at St. Petersburg. "What man in the world will ever believe that God Almighty should have introduced such confusion, or rather such shameful whoredom for the propagation of the reign of plants. Who would instruct young students in such voluptuous system without scandal." (See J. Trapp, *l. c.*, p. 121.)

‡ A. D. White, 'A History of the Warfare of Science with Theology', i, pp. 100-1 (1897).

§ Haller, resenting some remarks Linnaeus made about him in his 'Flora Suecica', 1745, retaliated by saying, in a critical review of the work: "The unbounded dominion which Linnaeus has assumed in the animal reign, must on the whole appear disgusting to many persons. He considered himself as a second Adam, and gave names to all the animals with their distinctive marks, without ever caring for his predecessors. He can hardly forbear to make *man a monkey*, or *the monkey a man*." (See J. Trapp, *l. c.*, p. 117.)

name we use ; but I demand of you, and of the whole world, that you show me a generic character—one that is according to generally accepted principles of classification—by which to distinguish between Man and Ape. I wish somebody would indicate one to me. But if I called man an ape, or vice versa, I should have fallen under the ban of all the ecclesiastics. It may be that as a naturalist I ought to have done so.”

Linnaeus was not a philosopher in the wide sense. He was far too busily engaged at the task in hand to be perpetually intent on abstract theory. His main object was systematizing the known species of plant and animal and describing them in a scientific terminology. Geographical exploration had been followed by the accumulation of vast masses of natural history material, and it was Linnaeus's great achievement to give to the world a convenient nomenclature and a practical classification. If it can be said of anyone that he brought order out of chaos it is most applicable to Linnaeus : *Deus creavit, Linnaeus disposuit*. Previous writers had gradually evolved the idea of genus and species from the common stock of knowledge. Tournefort was apparently the first to set forth clearly the characters of genera and Linnaeus in the same way clearly put forward the characters (or differentia) of species, and this in such a satisfactory manner that it is still customary to speak of the Linnaean species. Linnaeus's ideas were formally set out in his 'Fundamenta Botanica' in 1736, when he was twenty-nine years old. This is a series of 365 aphorisms : those dealing with descriptive terms were explained and expanded in 'Critica Botanica' the following year ; an English translation of this has been published recently by the Ray Society. The similar work relating to definitions was not published until 1751 as 'Philosophia Botanica', and naturally it is to this that we turn for the ideas with which Linnaeus's name is universally associated. He repeats the definition of species from 'Fundamenta Botanica' : We reckon as many species as there were diverse forms created in the beginning. (Species tot numeramus, quot diversae formae in principio sunt creatae.) He adds from 'Classes Plantarum' : Species are as many as there were diverse forms produced by the Infinite Being* ; which forms according to the appointed laws of generation, produce more individuals but always like themselves. Therefore there are as many species as there are different forms or structures occurring today. (Species tot sunt, quot diversas formas ab initio produxit Infinitum Ens ; quae formae,

* In the sixth edition of 'Genera Plantarum', 1764, constant is added to diverse. (Species tot sunt, quot diversas et constantes formas in hoc globo produxit Infinitum Ens.)

secundum generationis inditas leges, produxere plures, at sibi semper similes. Ergo species tot sunt, quot diversae formae s. structurae hodiernum occurrunt.) A new paragraph says: Uninterrupted succession, propagation, daily observations, cotyledons* make it impossible that new species are met with in plants. (Novas Species dari in vegetabilibus negat generatio continuata, propagatio, observationes quotidianae, Cotyledones.) A further paragraph says that those who have doubted this (dubium movere) are Marchant, Linnaeus, and Gmelin; a list of reputed hybrids is added.

Similarly, his definition of genera is adapted† from 'Fundamenta Botanica': We say there are as many genera as there are similarly constituted fructifications [flowers] of different natural species. (Genera tot dicimus, quot similes constructae fructificationes proferunt diversae Species naturales.) From 'Systema Naturae' he adds: Every genus is natural, created as such in the beginning hence not to be rashly split up or stuck together by whim or according to anyone's theory. (Genus omne est naturale, in primordio tale creatum, hinc pro lubitu & secundum ejuscumque theoriam non proterve discindendum aut conglutinandum.)

In another paragraph he says: Species are most constant, since their generation is a true continuation. (Species constantissimae sunt, cum earum generatio est vera continuatio.)

It would be difficult to find a more categorical affirmation about the fixity or constancy of species; they were all created in the beginning, they do not change, nor have they been added to‡.

* The term cotyledon was introduced into Botany by Linnaeus and was especially applied by him to those seed-leaves which do not act as food-stores but as organs of absorption, in which he saw an analogy in function to the placenta in Zoology. Starting from Harvey's dictum "omne vivum ex ovo" Linnaeus argued that as vegetables are obviously alive they also arise from eggs: the seeds are the eggs as appears by their producing offspring similar to the parent plant. The cotyledons of animals proceed from the yoke of the egg, on which is produced the speck of life: therefore the seminal leaves, in which is wrapped up the carculum, or essence of the seed, are also cotyledons. The 'proof' supplied by the cotyledons may be better understood if the cotyledon is taken to signify the embryo. Seeds are not formed unless a flower is fertilized. The occurrence of an embryo within the seed, brought about by the fusion of male and female, gives the certainty of continuous similarity or fixity.

† Linnaeus does not always repeat his own definitions exactly; there are occasionally slight modifications in words and punctuation.

‡ Cf. *Critica Botanica*, "All species reckon the origin of their stock in the first instance from the veritable hand of the Almighty Creator: for the Author of Nature, when He created species, imposed on his Creations an eternal law of reproduction and multiplication within

As has been indicated 'Fundamenta Botanica' was published in 1737, 'Philosophia Botanica' not until 1751. Meanwhile, however, several other writings of Linnaeus had appeared. One of the most interesting is an Oration, 'De Telluris Habitabilis Incremento', which he delivered in 1743 at the conferring of a medical degree, much of it being repeated in the preface to the 'Museum Regis Adolphi Friderici' in 1754. He believes that there was only one pair of every living thing created in the beginning. We are sure of this for the human species according to Moses's account, and that this first pair was placed in Eden where Adam gave names to all the animals. Now for him to have been able to do this all the species of animals must have been in Paradise which was not possible unless the species of plants had been there also, because of the nature of their food, particularly that of insects, examples of which he gives which are able to live upon one plant only. If the world had been formed in its present state all the species of animals must have been dispersed over the globe as they are at present, in which circumstances Adam could not have given names to them. But these difficulties vanish if we suppose that at the beginning all the world was covered with sea except one island large enough to contain all animals and plants. This supposition, he says, will appear highly reasonable, if we consider that the earth has been and is still gaining upon the sea. He gives facts about the finding of fossil shells on his travels, which he holds cannot be accounted for by the deluge: it is not credible that the Creator of the world should fill the earth with animals only to destroy them all shortly afterwards through the deluge, with the exception of a single pair of each species preserved in the Ark. This hypothetical island might have a soil and climate proper for all animals and plants by supposing it placed at the equator and crowned with a very high mountain. He states it as well known that the same plants are found on

the limits of their proper kinds. He did indeed in many instances allow them the power of sporting in their outward appearance, but never that of passing from one species to another. Hence to-day there are two kinds of difference between plants: one a true difference, the diversity produced by the all-wise hand of the Almighty, but the other, variation in the outside shell, the work of Nature in a sportive mood. Let a garden be sown with a thousand different seeds, let to these be given the incessant care of the Gardener in producing abnormal forms, and in a few years it will contain six thousand varieties, which the common herd of Botanists calls species. And so I distinguish the species of the Almighty Creator which are true from the abnormal varieties of the Gardener: the former I reckon of the highest importance because of their author, the latter I reject because of their authors. The former persist and have persisted from the beginning of the world, the latter, being monstrosities, can boast of but a brief life."

the Swiss, Pyrenean, and Scotch mountains. Mounts Olympus, Lebanon, and Ida, as on the mountains of Lapland and Greenland. Further Tournefort found at the base of Mt. Ararat the common plants of Armenia, a little higher up those of Italy, then those which grow about Paris, afterwards the Swedish plants, and on the summit the alpine plants of Lapland. He next considers how the single pair of each plant species might spread. First, there is the geometrical rate of increase. After giving examples of plants producing numerous seeds it is pointed out that even if only two seeds were to germinate each year these would give a population of 1,048,576 in twenty years, and we have also to take into account various methods of vegetative reproduction. The special adaptations for seed-dispersal are described and the ability of seeds to withstand inclement conditions. He seems to be approaching the idea of a struggle for existence, as he mentions among other matters that many plants are protected against animals by spines, prickles, thorns, and other means, and remarks on the mimicry of the fruits of *Medicago* and the seeds of *Salicornia* and *Salsola* to snails, preventing them becoming a prey to birds and fishes. Though at a later date he speaks of *Bellum omnium in omnes* * he was concerned here apparently only with the spread of plants from the creative centre. In one of his last paragraphs, however, he mentions the balance between herbivorous and carnivorous animals, birds, fishes, insects, and the animal and vegetable kingdoms. Among the many facts of interest commented on is the work of earth-worms, hedgehogs, moles, and swine in preparing the soil for the reception of seeds.

To return to 'Philosophia Botanica' we find that varieties are defined as in the 'Fundamenta', where Linnaeus had in mind chiefly what are now known as variations. There are as many varieties as there are different plants, produced from the seed of the same species. (Varietates tot sunt, quot differentes plantae ex ejusdem speciei semine sunt productae.) He adds that a variety is a plant changed by an accidental cause due to the climate, soil, heat, winds, etc. It is consequently reduced to its original form by a change of soil. (Varietas est Planta mutata a caussa accidentali: Climate, Solo, Calore, Ventis, &c., reducitur itaque in Solo mutato.) Further, the kinds of varieties are size, abundance, crispation, colour, taste, smell. (Species varietatum sunt Magnitudo, Plenitudo, Crispatio, Color, Sapor, Odor.) Species and genera are regarded as always the work of Nature, but varieties as more usually owing to culture. (Naturae opus semper est Species & Genus; culturae saepius

* 'De politia Naturae' (H. C. D. Wilcke), 1760.

Varietas.) * For that reason he would have ignored them in the general discussion of his ideas "published for the sake of my pupils", but that they often have economic, artistic, and medicinal uses.

So far as I have been able to discover, Linnaeus's statements about the fixity of species are the most definite made up to his time, for most writers who mention the matter are concerned only with the Creation, and invariably give some qualifying statements when dealing with species. I trust I shall not be misunderstood if I say that Linnaeus's general ideas about fixity were on the whole those which even a modern systematist would be prepared to accept, for if there were not some degree of fixity it would not be possible for their work to continue: the Linnaean Collections for example would cease to have any but historical value.

But it is not reasonable to judge Linnaeus's ideas solely by his didactic 'Philosophia Botanica'. His greatest botanical work, his Golden Book, *maximum opus et aeternum*, is 'Species Plantarum' published two years later. We know from his correspondence that he had been engaged upon the writing of this off and on for about nine years and consequently would not expect to find any departure from the definitions put forth in the 'Philosophia'. However, 'Philosophia Botanica' is precept, 'Species Plantarum' practice. In defining all described species he occasionally mentions the difficulty he has encountered. Turning to the genera *Salix*, *Rosa*, *Rubus*, *Hieracium*, as likely to have given trouble we find it recorded of *Salix* that the species are difficult to distinguish, their form being astonishingly changed by marshy, sandy, high, or hot ground so that botanists are often puzzled by them—and adds that the existing descriptions are imperfect and barbarous. (Species hujus generis difficillime extricantur. Solum palustre, arenosum, alpestre, calidum mutavit mira metamorphosi species, ut de iisdem haesitarint saepius Botanici; accessit Descriptio ubique imperfecta & barbara.) To *Salix triandra* there is a note: closely allied to the preceding [*S. hermaphroditica*] and the following [*S. pentandra*] species. (Perquam affinis ante-

* Cf. *Critica Botanica*, "All the species recognized by Botanists came forth from the Almighty Creator's hand, and the number of these is now and always will be exactly the same, while every day new and different florists' species arise from the true species so-called by Botanists, and when they have arisen they finally revert to the original forms. Accordingly to the former have been assigned by Nature fixed limits, beyond which they cannot go: while the latter display without end the infinite sport of Nature.

"The species of Botanists come from the All-wise hand of the Almighty, the varieties of Florists have proceeded from the sport of Nature, especially under the auspices of the Gardeners."

cedenti & sequenti.) Under *Rosa indica* he writes: The species of *Rosa* are difficult to distinguish and more difficult to determine: it seems to me that nature has intermingled several or by sport formed several from one. (Species Rosarum difficile distinguuntur, difficiliter determinantur: mihi videtur naturam miscuisse plures vel lusu ex uno plures formasse): he goes on that it is therefore easier for those who examine a few species to recognize them than for those who examine many. Of *Hieracium paludosum* he says that it is perhaps only a variety of *H. murorum*, although its very different appearance results from its environment. (Varietas forte sola antecedentis, quamvis ex loco evasit facie diversissima.) *Rubus* gives no obvious signs of taxonomic difficulties.

Scattered through the work are other notes which suggest the trend of Linnaeus's thoughts. *Thalictrum lucidum* has the note: Is the plant sufficiently distinct from *T. flavum*? It seems to me a daughter of time. (Planta, an satis distincta, a *T. flavo*? videtur temporis filia), i.e. a species of moist northern regions has given rise to one of sunny plains, rather than the reverse: an example of the fact that the known is usually assumed to be the original.

He queries whether *Achillea alpina* of the Siberian mountains has been produced from the lowland *A. Ptarmica* by environmental conditions. (An locus potuerat ex praecedenti formasse hanc?) In a note on *Plantago maritima* he remarks on the close affinity between this and five other species of *Plantago* (*P. lagopus*, *P. albicans*, *P. alpina*, *P. cretica*, and *P. subulata*), and wonders what force of nature might have produced their difference—habitat or hybridization? (Basis foliorum pilosa est, unde affinitas summa specierum 6.7.8.9.11, sed quae vis naturae efficeret tam varia? an locus: an copula.) *Lotus tenuifolia* is described as a variety of *Lotus corniculatus* with stems twice as long, linear leaves, and narrower pods: it seems to have originated in the shade (videtur in umbra nata), and the same origin is given for var. β of *Silene rupestris*. But habitat certainly does not suffice to explain the three constant varieties of *Serratula alpina* (planta floribus distinctissima, foliorum figura diversissima: sed quae causa produxerit has constantes varietates? certe locus non suffecerit), and doubt is expressed about *Drosera longifolia* which grows everywhere in Europe with the preceding [*D. rotundifolia*]: is it therefore a sufficiently diverse species? (Habitat in Europa ubique cum praecedente: an itaque satis diversa species?) If Linnaeus was convinced about the fixity of species he could not have been puzzled about two *Droseras* growing in the same habitat.

A very striking instance is the genus *Scorpiurus*. After describing the four species, he says: It is beyond all

doubt, that all these formerly arose from a single species, and the alteration in the environment is not sufficient for their creation: what commingling has then given rise to the constant plants? (Species hasce omnes olim ex una specie ortas esse dubium non est, nec sufficit locus harum generationi, qui tum mutatus easdem redderet; quae itaque mixtura harum produxerit constantes plantas?) There are similar ones as where concerning three species of *Geranium* he writes: The flower and habit of the three last plants [*G. cicutarium*, *G. malacoides*, and *G. gruinum*] show that at the beginning they were one. (Docet Fructificatio & habitus tres ultimas plantas ab initio unam fuisse, ortas procul dubio ex miscela diversarum, ut pro eadem haberi possent; at vero posse etjam distingui distinctas arbitrarium videtur); and under *Calendula* it is queried whether *C. hybrida*, *C. nudicaulis*, and *C. graminifolia* formerly arose from *C. pluvialis* as suggested by their habitat, seeds, and colour of the corollas. (Anne hae posteriores 3.4.5. e *C. pluviali* olim ortae sint? Sic suadet locus, semina, color corollae, habitus.)

Sonchus palustris is different in appearance from *S. arvensis* and yet structurally it is the same as if *S. palustris* formerly arose from *S. arvensis*. (Facies a *S. arvensi* diversissima: Structura tamen ita eadem, ac si *S. palustris* ex *S. arvensi* olim ortus fuisset.) That *Campanula hybrida* formerly arose from *C. Speculum* scarcely seems doubtful. (Quin haec ex *C. Spec.* ♀ olim orta sit, dubium vix videtur.)

Many notes suggest the hybrid origin of species or varieties. Five varieties of *Solanum nigrum* appear to be the offspring of hybrids (tot varietates β.γ.δ.ε.ζ. videntur esse hybridae proles): the varieties of *Citrus Medica* are to-day very numerous by the commingling with *C. Aurantium* (varietates hujus hodie numerosissimae una cum sequenti mixtae, de quibus Hesperides consulendae): he states that the varieties between *Fumaria spicata* and *F. capreolata*, judging from their flowers, might be considered as *F. officinalis* and queries whether they are hybrids (varietates qui statuatur hanc cum sequente esse *Fumariae officinalis* vix erret, dictitante fructu. An hybridae?). *Lactuca sativa* has no habitat accorded to it, but is thought to be produced by cultivation. (Culturae mangorico* forte producta ex proximis.)

Linnaeus frequently uses the word "affinis", with various qualifications, as for example, "nimis", "multa", "summa". If he was convinced of the fixity of species, could he have used such an expression with anything like its modern significance? Obviously not, for it would mean something beyond mere resemblance. Judging from some of his notes, however, it seems certain that he had in mind a true affinity. Thus he says of *Potentilla multifida* that close affinity with *P. argentea* is indicated by

* "mangonio" in 'Spec. Plant.', ed. 2.

its habit : that great affinity of *Cytisus supinus* with *C. hirsutus* is shown by the structure of the flower ; that the throat of the corolla of *Dianthus arenarius* proves its close affinity with *D. plumarius*. What may be regarded as conclusive is that this affinity is occasionally only "suspected", as that of *Polypodium comosum* with *P. phyllitidis* and *P. trifurcatum*, and that sometimes doubt is expressed whether a species is closely allied to or only a variety of another, as, for example, *Cheiranthus fenestralis* to *C. incanus*, or possibly a hybrid as *Gentiana campestris* (præcedenti [*G. Amarella*] nimis affinis & fere varietas aut hybrida).

Perhaps equally striking is the treatment of varieties in 'Species Plantarum' when we bear in mind the definitions repeated two years previously. Far from being merely variations in non-essential characters, they are treated in the same way as species, and as may be seen from some of the quotations already given it is sometimes queried whether what is described as a species is only a variety or vice versa. Constancy is now one of the characteristics : thus var. β (*fulvus*) of *Hemerocallis Lilio-Asphodelus* is described as "hybrida & constans", and the vars. α and β of *Adonis annua* remain distinct, though their structure is the same. Varieties may differ greatly according to their habitat as in vars. α and β of *Arabis alpina* (mire varians ex loco planta), and are often regarded as a result of habitat or hybridization, which may even bring about degeneration, as in *Hibiscus Sabdariffa* var. γ , of which the characters "omnia indicant has vel loco, vel hybrido partu degenerasse".

How are we to regard this apparent change of view between 1751 and 1753 ? I think by denying that there had been one. That this is so is shown by the fact that his earlier writings contain similar notes. 'Hortus Cliffortianus', 1737, is remarkably fully annotated and contains much of interest in showing the development of Linnaeus's ideas. Even here varieties are treated for the most part as permanent forms and attached to their appropriate species (varietates ad species proprias reduxi). He often remarks on the change in appearance of a species according to its conditions of growth, as, for example, *Polygonum amphibium* * in its land and water forms and *Ilex Aquifolium* where the stolons emerge and give rise to new trees (mira metamorphosis ! tamen nec imbellem progenerant aquilae columbam ! tamen nec unica species alteram diversam producit) ; *Poa trivialis* varies wonderfully according to the habitat ; the varieties of *Echium vulgare* are almost as many as the individuals, and so on. Some forms are regarded as arising from cultivation. Under *Rosmarinus officinalis* he states his axioms, to recognize no

* For convenience the binary names of the species are used.

garden plant which may not be known wild (nullam dari plantam hortensem, quae non ullibi terrarum sit sylvestris, est Axioma) and culture is unable to change a species (culturam non mutare species est etiam Axioma). If *Rosmarinus sativus* is not spontaneous those who urge its treatment as a separate species must say where it grows. He repeats under *Beta* that it is axiomatic that all edible plants were produced from wild ones, and queries what species gave rise to *Lactuca sativa*, and under *Narcissus* he says that he will study to search out only the creations of the Omnipotent (ego solum creata omnipotentis rimare studeo). The giving of names to all garden varieties he calls "a hodge-podge" (*Colchicum*, *Cucumis*). There are many examples where a species is queried as entitled to varietal rank only (*Ononis spinosa*) or vice versa (*Carlina vulgaris* vars.). Many species are regarded as "valde affinis" (*Antirrhinum dalmaticum* and *A. triphyllum*) "admodum affinis" (*Origanum sipyleum* and *O. Dictamnus*) "maxima affinis" (*Conyza bifrons* and *C. squarrosa*). *Pulmonaria angustifolia* may be produced by environment or by nature (inquirendum sit num haec a loco diversa evaserit vel a natura distincta sit species). Diligence and art have produced varieties of *Pyrus*; of *Sesamum orientale* the different forms are "varietates, vel lusus, vel species"; the variety of *Saponaria officinalis* is not the least among all the varieties produced by the sport of nature (quae natura ludendo producit). The only hint of crossing, however, appears to be under *Tulipa* and *Brassica*. The varieties of tulips are attributed to cultivation, various soils, and the mixing of differences by crossing, so that there are no laws for distinguishing them; those of *Brassica oleracea* mix by crossing. (Hocque oriri statuit a miscela generationis.) He describes the male and female flowers of *Carica Papaya*, but regards them as the same species "inde tamen homo non separat, quae Deus conjunxit". Furthermore, genera are grouped, as for example *Annona*, *Magnolia*, and *Liriodendrum*, which are said to be "inter se valde affines".

'Flora Suecica' was published in 1745. Here again several species are regarded as related to others (*Sisymbrium amphibium*), or perhaps only varieties (*Fucus serratus*); an American *Pyrola* is regarded as a variety of a European species (ergo americana planta hujus varietas est). Varieties may be inconstant, as var. β of *Rhinanthus Crista-Galli*, the seeds of which when sown in a dry meadow produce the typical plant the next year (semina e planta β projecta in pratum siccum, proximo anno reddunt plantam α , hinc non opus fuisset duas species constituere), or constant as var. β of *Alnus* (antea diximus β esse varietatem ab α , & adhuc idem absolute statuimus, licet varietatem esse distinctam non negemus).

In 'Hortus Upsaliensis' published in 1748 there are further notes. Thus *Phillyrea* 2 is said to be very closely related to *Phillyrea* 1 (valde affinis praecedenti), *Solidago* 2 very closely related to *Solidago* 1, and *Syringa* 3 is perhaps only a variety of *Syringa* 2 (forte antecedentis sola varietas). Under *Hyoscyamus* 2 it is queried whether new plants can arise by hybridization and whether these hybrid species can propagate. The future would show. (An oriantur novae plantae ex diversa copula? an Hybridae speciem propagant?.... Serus dies determinabit.) Of *Dracocephalum* 6 he says that it is perhaps only a hybrid from *Nepeta* 3 (haec forte hybrida ex *Nepeta* 3) queries whether *Dracocephalum* 7 is a new hybrid (anne heic species novae e diversa copula hybridae?) and *Poterium* 2 a hybrid from *Poterium* 1 and *Agrimonia*.

Though it is obvious, therefore, that there was no change of view, we are still left with the problem of explaining the categorical statements in 'Philosophia Botanica'. Is not the explanation the simple one that this was a text-book, and that too much stress has been placed upon it both by Linnaeus's contemporaries and by those who thought that therein they had an epitome of his botanical philosophy? The series of aphorisms of 1736 were copied practically verbatim into 'Philosophia Botanica' years afterwards; the additional matter in small type must be regarded as subsidiary and explanatory, not altering the general meaning. 'Philosophia Botanica', remarkable as it is, suffered like many more modern text-books in being an enlarged second edition and as a students' book was concerned more with giving them a general account of certain aspects of botany at a stage where it was probably considered better to receive categorical statements than to wander into the realms of real philosophy. However this may be, it is a commonly adopted method to-day. There is the hint in 'Philosophia Botanica', where he names those, himself included, who have doubted the occurrence of new species, as if entering a caveat. That his students were not kept in the dark about his ideas is seen from their theses, 'Amoenitates Academicae', but these were written at the end of their university career.

Linnaeus early became convinced that plants had sexuality. This indeed was no new idea, for we find traces of it from the earliest times: artificial pollination was practised with the dioecious date palm at least as far back as the Babyionian period, and caprifigation is older than Herodotus.

It was by learning of Vaillant's inaugural address, given in 1717, when he succeeded Tournefort in the Chair of Botany at Paris, that Linnaeus turned his attention to the stamens and pistil, and found them more convenient distinguishing

marks than the petals. Linnaeus has left it on record that he learned of Vaillant's paper from a review; but from his earliest known botanical writing, which is on exhibit in our rooms, it appears that he heard of it during Rothman's private tuition before going to Lund in 1727. It has been stated that Linnaeus reached his ideas by scholastic reasoning, but this is a superficial judgment based on a few of his aphorisms and disregards his first paper on the subject which he wrote as a New Year's gift to his benefactor Celsius to refute an academic thesis which had appeared in 1729 on 'Nuptiae Arborum'.

Thereafter Linnaeus always took an interest in any observation on the biology of the flower and in hybrids, as is to be seen particularly in the 'Amoenitates Academicæ', the 186 academic disputations which bear his name, as well as that of the candidate. For our purpose we may assume that the ideas were those of Linnaeus, for it was then the practice for the professor to dictate the thesis to the pupil, who, having put it in order, argued it at a formal act of disputation at which the Professor presided. It is not surprising, therefore, that there is a good deal of repetition in them.

So early as 1744 in a thesis on *Peloria* (Daniel Rudberg) the problem of species-crossing in plants was discussed and several reputed plant hybrids listed. It was known that *Peloria* was related to *Linaria* and, by analogy with animal hybrids resulting from unnatural union, it was assumed that it was a hybrid with an unknown father.

"Moreover, it is a fact that different species have been bred in the vegetable kingdom of which few, or rather no, traces of antecedent times has experimentation laid bare. Nor can we perceive otherwise but that the *Peloria* came into existence by a fertilization of this sort. If the location, climate, or nourishment had effected this change, then on the same stalk we would see flowers, some more, some less, in accord with the structure of the *Linaria*. But this is not the case. For in all the individual flowers of the *Peloria*, so exact a peculiar likeness has been discovered that not even the larger one of the flowers of the *Linaria* has appeared. However, we confess that we do not know by what other flower the *Linaria* has been impregnated when it produces the *Peloria*, and this has been the final pronouncement of one who has observed the plants which bloom at the same time and in the same place as the *Linaria*. Besides it must be noted that in the flowers of the *Linaria* the neck is almost closed so that it would be very hard for it to admit the pollen of some other flower to fertilize its pistil unless the lips of the corolla had been torn and eaten away beforehand by insects. It seems on first sight a paradox that new species, nay, even new genera, should arise from the copulation of different species in the

vegetable kingdom ; meanwhile observations persuade us that this very thing takes place. Why all the cacti in America ? Why so many species of aloes and geranium at the Cape of Good Hope ? Numerous varieties of many species are being inspected attentively. . . . If it can be decided with certainty that the *Peloria* must have arisen as a hybrid species from the *Linaria* and some other plant, a new truth would come to light in the vegetable kingdom, and that process (i.e., hybridization) in the case of plants would be further advanced than in the case of animals in that animal hybrids, like Mules and others, lack the ability to propagate themselves. But we see that the *Peloria* propagates, for it has perfect seeds and in its natal place multiplies copiously and of its own accord. But future experimentation must investigate whether a *Linaria* is ever born from the seeds of the *Peloria*. But if, as seems probable from observations now made, this does not happen, but the *Peloria* remains constant, thence follows a mighty thesis ; it would become an undoubted fact that new species make their appearance in the vegetable kingdom ; that the genera may exhibit differences in fructification, but rejoice in one and the same nature and strength ; nay even, that one and the same genus may have diverse fructifications. By this thesis the fundamental principles governing fructification, which is the foundation of the whole science of Botany, would be destroyed, and it would infringe upon the natural classes of plants, to such an extent indeed that in our *Peloria* all who are skilled in our field would wonder, not without reason, at the stupendous fruit of Nature."

Although "*Peloria* is generated from *Linaria*" it is not due to crossing, nor to degeneration as Stehelin thought who first described and pictured a peloric flower on a plant with normal *Linaria* flowers. Nevertheless, it is remarkable that Linnaeus did not incorporate more of this line of thought in his '*Philosophia*' published seven years later. It may be that he was not interested at that time in hybrids as such, but only as proving his contentions about sex.

Another dissertation '*Sponsalia Plantarum*' was published in 1746 (Johannes Gustavus Wahlbom). Most of it is concerned with the sexual processes of plants, but it contains clear descriptions of hybridization in Tulips. "Experimentation in horticulture is a pleasant thing : If perhaps a man delight only in a red tulip, let him pull off all the anthers on one flower before the pollen is scattered, then let him take a tulip with a white flower and sprinkle the anthers of this over the stigma of the red one, then when the seeds are matured, let him plant them in their own garden, and he will produce flowers in this garden, some red, some white, and many other bicoloured, just as the offspring of two animals of

different colors is born adorned in various hues." The origin of the variations in tulip colour had been explained similarly in the last-mentioned thesis: that favoured by earlier writers, following Clusius, was that there was degeneration, the classical theory of spontaneous transmutation of species dating from Theophrastus. One of the best-known examples of reputed degeneration was first recorded by Robert Morison in his 'Plantarum Historia Universalis Oxoniensis,' 1680. "The same thing must be said of the *Brassica florida* Botrytis, seed of which was recently sent to us from India; it produced *Brassica florida*, but their seed, collected and sown in England, degenerate into the *Brassica longifolia et aperta*, a fact which experience has made known to all, but to no man more so than to Richard Baal, the gardener at Bramford, who collected in his own garden a large number of seeds from the *Brassica florida*, which he sold to gardeners, very many of whom lived in suburban districts of London, vulgarly known as 'Neat Houses', and these men committed those same seeds with the greatest care and industry to earth well fertilized by many years, but these seeds produced for them the large *Brassica longifolia aperta*! For this reason the aforementioned gardeners, noting that they had lost their work and their toil; that is, that they had expended their industry, care, labor, at great expense and without return, nay, with the greatest detriment and expenditure of time and money, started a lawsuit against the aforesaid Baal in the Court of Westminster and the decision of the Judges sitting there not only condemned him to restore to the men the money which he had received from them, but in addition that same Baal was fined that he might recompense the aforesaid gardeners for the waste of their time, their expense, and the use of their ground." In the dissertation we read, "The above described misdemeanor must not be ascribed to the gardener, Baal, but to the fact that his *Brassicæ optimæ* were impregnated by the *Brassica vulgaris*. Wherefore, if anyone possess a *Brassica optima* he must not let it flower in the same garden with another, lest the better one be fertilized by the pollen of the poorer one, and from these seeds a poorer stock be produced." Morison's account is repeated in the chapter on degeneration in Ray's 'Historia Plantarum', and was presumably taken from this by Linnaeus.

The statement in the thesis that "bees do more good than harm for they scatter pollen on the pistil" is sometimes regarded as the earliest observation of insect pollination, but Philip Miller had written to Richard Bradley and to Patrick Blair in 1721 describing the insect pollination of tulips and the sterility of unpollinated spinach flowers.

A dissertation which has received more attention than most

of the others was that on 'Plantae Hybridae' (Johannes J. Haartman), published in 1751. No experimental work is described in this, but a list is given of a hundred plants believed to be hybrids on taxonomic grounds: sixty of them are described. One of these is the well-known Alsike clover (*Trifolium hybridum*), a hybrid between *Trifolium repens* and *T. pratense* which originated spontaneously at Alsike near Uppsala and also near Aboa. It is stated that plants are so changed by the climate and the fertility of the soil that one and the same plant, born in different earth very often seems to be a variety entirely unlike its parents. "But if I am asked whether new species of plants can spring into being through mixing two distinct varieties, or whether they do appear daily, I would reply to these questions that in accordance with theoretic principles, and as far as we can discern with our eyes, I would freely declare my opinion by denying it." But he points out that "The chief argument for believing in hybrid plants, however, seems to be corroborated by the following. For all agree that Botanists such as Tournefort, Boerhaave, Mitchell, Pontedera, and Helwing, with the rest who lived at the end of the last century, and indeed in the time of our President in this century, have collected innumerable new European plants, unknown to the ancients, but it must be observed that these plants are for the most part so like the old ones that they can scarcely be distinguished by form. And so when differentiating characteristics were sufficiently absent, our President [Linnaeus] referred to their mother plant under the name of varieties, which differ in color, odor, taste, size, time of maturity, etc., and the most acute of the Botanists, like Jussieu, Ray, Gronovius, Haller, Gmelin, Guettard, Dalibard, Wachendorff, Gorter, Bütnner, etc., also approved this practice and continued it after him. Indeed it has been said that these varieties arise from the condition of their soil, place, or climate, and to that extent only are accidental. Meanwhile, however, to this reformation were subjected many plants, which had often been a source of the greatest anxiety to botanists in the determination of their species, and to which species they deserved to be referred, when they resemble two different species, especially when the distinguishing characteristics of the plant in question are found not to be unique, yet very distinct and very individual or absent in either of these two species they resemble. And this hybrid grows in the same soil with both the species and yet was not observed by the ancients. And this circumstance first led us by deduction to this problem, whether two different plants have produced a third and whether the third plant is to be considered a hybrid, for botanists have first recognized with clarity in these times of ours the principles governing

generation in plants, and such changes in plants may be deduced from what they have observed in the *Brassica* and others.

"Since nature is very opulent and various in her operations, I would almost believe nothing except that which can be shown by experimentation or can be touched with the hands, and therefore I now advance to the effects of nature, ready to examine whatever she has proved." Further, "It is not true that the varieties of plants arise from conditions of soil and hence can be changed by cultivation. The *Paeonia* or the double *Narcissus* is not changed by virtue of its soil into the single nor for that reason are they diverse in species. It is not strange that a hybrid which is the child of a swamp and a mountain plant should seek a third kind of soil. For this reason the grandfathers and great-grandfathers are sought in vain next to the daughter plant." It is suggested that on the basis of these hypotheses botanists not yet born may rear on its foundations a reformation in the whole science of Botany, and may distinguish the variety of species far differently, and perchance also genera.

'Somnus Plantarum' (Petrus Bremer), 1755, has the statement: "The flowers of some species are impregnated by the farina of different genera, and species, inasmuch that hybridous or mongrel plants are frequently produced, which, if not admitted as new species, are at least permanent varieties." 'Metamorphosis Plantarum', 1755 (Nicol. E. Dahlberg) incidentally mentions the same point, clearly showing the lines along which Linnaeus's mind was then working. "If now it is so (which seems very probable) that many hybrid plants are propagated by seed, they may occasionally achieve the status of the constant varieties, and for this reason a new metamorphosis in plants is effected.

"These constant varieties (to which *Sedum Telephium*, the *Serapias helleborine*, and many other plants belong), which are now disturbing Botanists very much*, may possibly be explained occasionally in accordance with the principle of sex in plants and hybrid generation". After describing what is presumed to be the product of some intermingling between *Pinus sylvestris* and *Pinus Abies* he records that *Lychnis apetala* is constant in the Lapland mountains, although it grows among *Lychnis dioica*. "Even when this is planted in gardens it is just as constant as in the Alps; we observe with ease that this plant today is distinct; however, it seems quite indubitable to me that it arose first from the *Lychnis dioica*, and especially because of a specimen gathered in Siberia by Dr. Gmelin, such as we do not possess within our own boundaries."

* Cf. 'Flora Suecica', ed. 2, p. 247, under *Fumaria* (also 1755): dantur enim innumerae varietates quae cultura non reducuntur, sed constantes persistunt.

'Generatio Ambigena' in 1759 (Christian. L. Ramstrom) describes an experiment by Linnaeus, who noticing a hybrid between *Tragopogon porrifolium* and *T. pratense* in the academic garden, pollinated the second species with pollen from the first and successfully reproduced the hybrid. "Perchance the day may come which will show that very many of the *Gerania Africana* and *Mesembryanthemata* and many species of the same genera are perhaps the product of that very circumstance, i.e., that a vagabond father (i.e., pollen carried by the air) has fertilized the mother plant. And although hybrids are often sterile, both in the animal and vegetable kingdoms, this is not, however, universally the case; but admits of many exceptions, at least in the *Tragopogon* named above. Hence on occasion botanists may have new rules, i.e., that as many species may be held to be congenerous as to have been produced from the same medullary substance of the mother. We are taught by the insects not to disturb this arrangement of Nature, for they eat up plants of the same genus which they have not seen before and which were but recently imported from India."

In 'Theses Medicae', 1760 (Johannes Christian. Daniel Schreber), granting the fact of hybrid plants, it is said that "it seems probable that plants which are similar in their fructification, though different in external structure, have descended from one and the same plant; but whether these are to be called the daughters of time, or whether they were mixed by their Creator in the beginning, a later day will show. Meanwhile, botanists have called these plants which are similar in their fructification, species of the same genus".

Although there is occasionally some doubt whether Linnaeus was wholly responsible for the statements appearing in the 'Amoenitates' there is fortunately a clear statement of his views in a dissertation on the sexes of plants which was published in 1760 ('Disquisitio de Sexu Plantarum'). This was the successful essay for a prize of one hundred ducats offered by the Imperial Academy of St. Petersburg for the best dissertation on the sexes of plants in which the doctrine was either to be confirmed or refuted by new arguments and experiments, besides those already known, an historical and physical detail being prefixed of all the parts of a plant supposed to have a share in impregnating and perfecting the fruit and seed. It was thought that the question was so proposed to draw forth Linnaeus's ideas.

After a summary of ancient beliefs about the date palm, fig, pistacia, and so on, and a mention of the opinions of recent writers the dissertation gives an account of several successful experiments on fertilization carried out in a thoroughly scientific manner. Only one refers to a hybrid, *Mirabilis*

longifolia pollinated with *M. Jalapa*. Four "real" plants are described however, "to whose origin I have been an eyewitness":—*Veronica spuria* (*Veronica maritima* ♀ × *Verbena officinalis* ♂), *Delphinium hybridum* (*Delphinium elatum* ♀ × *Aconitum Napellus* ♂), *Hieracium Taraxaci* (*Hieracium alpinum* ♀ × *Leontodon Taraxacum* ♂), *Tragopogon hybridum* (*T. pratense* ♀ × *T. porrifolium* ♂), of which seeds were sent.

About these plants Linnaeus says, "There can be no doubt that these are all new species produced by hybrid generation. And hence we learn, that a mule offspring is the exact image of its mother in its medullary substance, internal nature, or fructification, but resembles its father in leaves. This is a foundation upon which naturalists may build much. For it seems probable that many plants, which now appear different species of the same genus, may in the beginning have been but one plant, having arisen merely from hybrid generation. Many of those *Geraniums* which grow at the Cape of Good Hope, and have never been found wild any where but in the south parts of Africa, and which, as they are distinguished from all other *Geraniums* by their single-leaved calyx, many-flowered foot-stalk, irregular corolla, seven fertile stamina, and three mutilated ones, and by their naked seeds furnished with downy awns; so they agree together in all these characters, although very various in their roots, stems, and leaves; these *Geraniums*, I say, would almost induce a botanist to believe, that the species of one genus in vegetables are only so many different plants as there have been different associations with the flowers of one species, and consequently a genus is nothing else than a number of plants sprung from the same mother by different fathers. But whether all these species be the offspring of time; whether, in the beginning of all things, the Creator limited the number of future species, I dare not presume to determine. I am, however, convinced, this mode of multiplying plants does not interfere with the system or general scheme of nature; as I daily observe, that insects, which live upon one species of a particular genus, are contented with another of the same genus". He ends his essay thus: "Here is a new employment for botanists, to attempt the production of new species of vegetables, by scattering the pollen of various plants over various widowed females. And if these remarks should meet with a favorable reception, I shall be the more induced to dedicate what remains of my life to such experiments, which recommend themselves by being at the same time agreeable and useful. I am persuaded by many considerations, that those numerous and most valuable varieties of plants which are used for culinary purposes, have been produced in this manner, as the several kinds of cabbages, lettuces, &c.; and

I apprehend this is the reason of their not being changed by a difference of soil. Hence I cannot give my assent to the opinion of those, who imagine all varieties to have been occasioned by change of soil; for, if this were the case, the plants would return to their original form, if removed again to their original situation."

His final sentence shows his original interest, "That the sexes of plants admit of a proof *a priori* from experiments, appears therefore from hybrid productions."

'Fundamenta fructificationis' (Johannes Mart. Gråberg), 1762, the year after the appearance of the first of Koelreuter's classical papers on the sex of plants, also deals with hybrids, but adds little from our point of view. "It is indeed true that numerous hybrid plants do not propagate the species through the seeds, but it nevertheless does not follow that all hybrids are sterile. . . . In a word, when the stigmas of any plant are sprinkled with foreign pollen, in some cases nothing occurs; where such fecundation succeeds, there proceed from these plants, when sown, plants called hybrids. . . . These hybrids, thus born, are either fertile as *Delphinium aconite*, *Tragopogon hybridum*, etc., or persist simply sterile like mules, and if they flower they nevertheless produce no seeds, as *Verbascum Thapsus*, *Veronica Verbenae*, etc. The flowers of these sterile plants being examined, the anthers are observed to be sterile, destitute of any pollen" *.

Here we find a later theory of the Creation. "We imagine that the Creator at the actual time of creation made only one single species for each natural order of plants, this species being different in habit and fructification from all the rest. That he made these mutually fertile, whence out of their progeny, fructification having been somewhat changed, Genera of natural classes have arisen as many in number as the different parents, and since this is not carried further, we regard this also as having been done by His Omnipotent hand directly in the beginning; thus all Genera were primeval and consisted of a single Species. That as many Genera having arisen as there were individuals in the beginning, these plants in course of time become fertilized by others of different sort and thus arose Species until so many were produced as now

* To minimize the risk of so translating Linnaeus's words that the point of view put forward in this address should receive false support I have used existing translations where possible. That of the letter to Gmelin (p. 195) is from E. L. Greene's 'Carolus Linnaeus'; those from 'Critica Botanica' are from A. Hort's translation; those of the 'Amoenitates Academicæ' are from C. Zirkle's 'The Beginnings of Plant Hybridization' except the above, the first part of which is from H. F. Robert's 'Plant Hybridization before Mendel'; that of Linnaeus's 'Disquisitio de Sexu Plantarum' (p. 211) is from J. E. Smith's translation.

exist.... That also some Genera multiplied into very numerous Species.... That these Species were sometimes fertilized out of congeners, that is other Species of the same Genus, whence have arisen Varieties." The same theory of progress from simple to compound, from few to many (e simplice progressus ad composita ; e paucis ad plura !) was repeated in the sixth edition of 'Genera Plantarum', 1764.

We may think no more highly than did Sachs of this philosophy, but his remark that "Apart from some insignificant verbal explanations, Linnaeus adduced nothing in support of the dogma but the every-day perception of the unchangeableness of species, and to this he held fast to the end of his life" is simply untrue.

The second edition of 'Species Plantarum' was published in 1762-3. There are additional notes to those given in the first edition. One is struck by the greater number of species which are regarded as "affinis" to other species of the same genus. Also "filia" is much more common and occasionally we find "soror". *Hibiscus Pentacarpus* which inhabits the Venetian marshes perhaps arose from *H. virginicus* (forte a praecedenti orta ?) which occurs in salt marshes in Virginia—a somewhat far cry ; *Urtica balearica* is strongly allied to *U. pilulifera*, and is perhaps a variety or daughter of it—an Indian species derived from a South European one (forte varietas vel filia prioris) and similarly *Musa sapientum* is a natural daughter or hybrid with Bihai as mother (planta etjam filia naturalis s. hybrida Matris Bihai). The cultivated *Beta vulgaris*, which has no habitat given as it is not known in the wild, and of which seven varieties are listed, is possibly born of *B. maritima* in a foreign land (forte a *maritima*, in exoticis, prognata). The hybrid origin of several species described in the 'Amoenitates' is also mentioned—*Sorbus hybrida* is a hybrid between *Crataegus Aria* and *Sorbus Aucuparia*, but propagates as a distinct species. (Nova arbor e *Crataego Aria* β & *Sorbo Aucuparia*, sed speciem distinctam propagans.) *Rumex tuberosus* is very closely related to *R. Acetosa* as if it was a hybrid of it (Affinis nimium *R. Acetosae* ac si ejus hybrida) and *Bupleurum semicompositum* is related to *B. Odontites* yet scarcely to be regarded as a variety (affine *B. Odontiti*, vix tamen pro varietate assumendum), and so on. The three species of *Basella* are closely related, but prove constant in gardens (Affines nimium sunt hae tres Species, sed constantes se servant in hortis), but *Primula veris* is treated as a collective species including *P. officinalis* (α), *P. elatior* (β), and *P. acaulis* (γ), and the Roman colony of Mauretania in NW. Africa is mentioned as an analogy for not distinguishing the varieties β , γ as species (Varietates licet constantes β . γ . non specie distinguo, uti nec Maurum ab

Europaeo). Three species of *Cleome*, *C. heptaphylla*, *C. pentaphylla*, and *C. triphylla* formerly arose from the same plant as shown by various characters and are therefore scarcely sufficiently diverse species. (Tres praecedentes (2, 3, 4,) ex eadem planta olim prognatas evincunt Folia . . . vix itaque specie sufficienter diversae.) He says concerning the species of *Rosa* that their limits are hard to circumscribe and that perhaps nature herself scarcely lays them down (Species Rosarum difficillime limitibus circumscribuntur & forte natura vix eos posuit), an example of the "diffusiora genera" or "prolixiora genera" described in 'Plantae Hybridae' in contrast to the usual sharply defined species (a natura distincte determinatae).

Linnaeus's practical acquaintance with plants was obtained not only from his botanical travels to Lapland, Dalecarlia, Öland, and Gotland, and visits to foreign gardens, but also from sowing thousands of seeds every year from all parts of the world, as we learn from 'Transmutatio frumentorum' (B. Hornborg). (Debet Hortos intrare Academicos, ubi millena semina, quotannis e plagis remotissimis orbis advecta, seruntur, & videre, quod singula promant suam plantam, nec aliam.)

One other aspect of Linnaeus's work bears on his ideas of species. When in his early twenties he was inspired by Vaillant's discourse to examine more closely the stamens and pistils of flowers, he found therein a certain and ready means of differentiation. He invented his so-called Sexual System as early as 1731 (when he was 24) and published it in his 'Florula Laponica' in 1732, arranging all known plant-genera by it in 'Systema Naturae', 1735. The system is based on the number, situation, proportion, or connexion of the stamens and pistil. Its sole object was to enable the identification of any described plant by an analytical method—a method which is applied absolutely except that it is not allowed to divide a genus so that sections fall into different parts of the system. As in all previous systems some nearly related genera occur in proximity.

Linnaeus from the beginning was intent on finding out a more natural method, i.e. a more philosophical classification. In 'Fundamenta Botanica', 1736, he mentions his resolve to attempt a fragment of a method. The following year in 'Genera Plantarum' he does this, repeating the fragments in his 'Classes Plantarum', 1738, where, after giving an account of the different classifications which had been proposed up to that time, he lists related genera in 65 orders, which are not given names, but numbers: they include Cryptogams and Sponges, with questions about inclusions and occasional notes about affinities. He says that the

Alpha and Omega to be sought in Systematic Botany is a natural method (*Primum & ultimum in parte Systematica Botanices quaesitum est Methodus Naturalis*) and adds: For a long time I have laboured to find it; I have discovered many things, but I have not been able to accomplish it. I shall continue it as long as I live. In the meantime, I shall publish what I have learned. He who will solve the few doubtful plants that remain will be for me the great Apollo. (*Diu & Ego circa methodum naturalem inveniendam laboravi, bene multa quae adderem obtinui, perficere non potui, continuaturus dum vixero; interim quae novi proponam; qui paucas, quae restant, bene absolvit plantas, omnibus magnus erit mihi Apollo.*) He declared that he could find no certain principle or key to define the orders by characters until all the plants in the world are known. In the corresponding section of '*Philosophia Botanica*' he lists 67 natural orders which are reduced to 58 in the 6th edition of '*Genera Plantarum*', 1764, where he states: Natural orders serve to teach the nature of plants, artificial ones to distinguish one plant from another. (*Ordines naturales valent de natura plantarum artificiales in diagnosi plantarum.*) Linnaeus, as we see from manuscript notes in his own interleaved copies of his writings, constantly worked at the Natural System, basing his ideas mainly on what he called the simple symmetry of all parts. Although previous botanists had to some extent grasped the idea of a natural system, it was Linnaeus who clearly distinguished between this and an artificial system. As a result of the facility and certainty of determination which his artificial system provided, his name is most closely associated with that, though he himself expected it to be replaced. (*Perpetuum est, quod methodus artificialis sit tantum naturalis succedanea, nec possit non cedere naturali, si detegeretur.*) After his death his pupil Giseke compiled an account of Linnaeus's Natural System from his own notes and those of Fabricius of the lectures Linnaeus was accustomed to give on the subject*. Linnaeus early conceived the idea that natural orders are related in the same manner as different territories in a geographical map. (*Plantae omnes utrinque affinitatum monstrant uti Territorium in Mappa geographica.*) Giseke gives a pictorial representation of this idea, which has the appearance of the more recent rather than the classical phylogenetic trees.

In this sketch of Linnaeus's views many points which bear on them have had to be omitted, and I am fully conscious of not having garnered all the fruits in his store. However, without in any way attempting to read into his statements more than he himself meant we see clearly that his

* L. J. Montin's manuscript note-books of Linnaeus's Lectures are in the Department of Botany, British Museum.

view on the fixity of species changed considerably and that he soon came to believe in the production of new species as well as new varieties by hybridization, by the effect of environment and by cultivation. He removed the statement "*nullae species novae*" from the preface to the 1766 edition of '*Systema Naturae*' and crossed out "*Natura non facit saltus*" in his own copy of '*Philosophia Botanica*'; and we may add that a comparison of some of the specific descriptions in the two editions of '*Species Plantarum*' shows that he no longer believed in species being so fixed that they could be differentiated by a single short expression. Much can also be made of his ecological grouping of species and of his recognition of adaptation to environment. He rejected the idea of Spontaneous generation—if minute organisms could be produced from putrefaction and hatched out by the heat of the sun why not horses and elephants? Moreover, from the first he regarded his Sexual System as one of convenience until the time when a Natural System could take its place, though admittedly he thought this time far distant.

How are we to account then for the views about Linnaeus prevalent for more than a century? The only explanation seems to be that botanists and zoologists were mainly occupied in accumulating and naming collections. In this botanists at least found their only hope in the use of Linnaeus's sexual system and his binary nomenclature. They dreaded the unutterable confusion that would follow the breaking down of these. Any attempt to introduce a natural system was at first resisted with as much vehemence as would have met an attack on Linnaeus's nomenclature and terminology. It was his detailed descriptive works that had to be protected—otherwise all would be chaos. After the old doubts all seemed certain and fixed. His early views as enshrined in his elementary text-book '*Philosophia Botanica*' were easy of access and readily understood. They gave comfort to the orthodox both in theology and in taxonomy: species were created as they now exist. And so systematists worked on that principle even when they developed his ideas on a natural classification. Bernard de Jussieu, friend of Linnaeus and sub-demonstrator to the Chair of Botany occupied by his brother at Paris, arranged the flower beds in the garden of Trianon in 1759 on a natural system. His catalogue was published in 1789 by his nephew Antoine Laurent, who pointed out that the system was based on the principle of the subordination of characters. A. L. de Jussieu gave the characters of a hundred natural orders and these form the basis of the modern classification of flowering plants. The natural system was further elaborated by De Candolle in 1813, who based his characters mainly on the symmetry of the parts

of the flowers, recalling Linnaeus's opinion expressed in 'Classes Plantarum', 1738, and uses the deviations brought about by abortion, degeneration, and adherence in arranging his groups. His idea of a plan of symmetry is much the same fundamentally as the type concept of zoologists which reigned in the first part of the 19th century. But though the idea of an original plan necessarily postulated changes by abortion these were not considered inconsistent with the concept of immutability. Robert Brown in this country adopted de Jussieu's classification in his 'Prodromus' (1810). By his monographic studies he did a great deal to establish a natural system by shedding light on the systematic value of morphological characters as opposed to physiological functions.

Robert Brown died June 10th, 1858. According to the Charter of this Society a special meeting had to be held within three calendar months to fill the vacancy thus caused on the Council. To avoid holding a meeting in the recess it was called for July 1. Bentham, who was elected, has recorded that "a long paper of mine had been set down for reading, in which, in commenting on the British Flora, I had collected a number of observations and facts illustrating what I then believed to be a fixity in species, however difficult it might be to assign their limits, and showing a tendency of abnormal forms, produced by cultivation or otherwise, to withdraw within those original limits when left to themselves". It was at this meeting that J. D. Hooker and Charles Lyell communicated the accounts of Natural Selection by Darwin and Wallace. Bentham, ignorant till then of Darwin's theory, felt bound to defer his paper for reconsideration.

In a letter to one of the first three nominated Honorary Members our first President, Sir James Edward Smith writes: "The Linⁿ Soc^y is a body of naturalists associated for the purpose of cultivating the science, not to enlist themselves as the followers of any person whatever, any further than truth directs them. They have taken the name which you unfortunately dislike, but w^{ch} I do not think w^d readily change, unless it were generally disapproved, nor should I soon be brought to consent to such an alteration. We have always conceived this name peculiarly proper for us, who have among us the very museum & Lib^y of Lin^s in the house where we meet.... We consider his works as a good foundation to work upon, we are best able to determine the different objects he described, to correct his errors & improve what he has left imperfect. On this ground we call ourselves the Linⁿ Soc^y, and I hope you will not think it an improper one." In his Introductory Discourse on April 8th, 1788, the President, whose property the Linnaean collections then were, said, "For my own part I consider myself as a trustee

of the public. I hold these treasures only for the purpose of making them useful to the world and natural history in general". After 150 years the Linnean Society fully endorses this as its own standpoint and will continue its trust of the treasures left by the immortal Swede, Carl von Linné. We believe we have adequately arranged for their safety if the noise of war should again reach our shores. When last there was danger the herbarium was moved from the three wooden cases in which it had remained since its arrival in this country. It seemed to us that the present would be a fitting occasion on which to return two of these cases to Sweden—one to the Swedish Linnean Society and one to the Museum at Hammarby. I would ask Professor Robert Fries, President of our sister Society, and son of T. M. Fries, Linnaeus's biographer and the restorer of Hammarby, to accept them on their behalf.

Professor Robert Fries then received the keys and thanked the Society.

Lieut.-Col. Sir DAVID PRAIN, C.I.E., C.M.G., F.R.S., F.L.S., moved that the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated among the Fellows. The motion was seconded by Sir SIDNEY HARMER, K.B.E., F.R.S., F.L.S., being put to the meeting by Sir David Prain it was carried with acclamation.

STATUTORY ANNIVERSARY MEETING

The Society met in closed session at 5.0 p.m. on 24 May in Burlington House, Piccadilly.

Mr. J. RAMSBOTTOM, O.B.E., Dr.Sc., President,
in the Chair

The Proceedings of the previous meeting, held on Thursday, 5 May 1938, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Harry Arnold Baylis, Hans Theodor Güssow, Harold Hart Mann, and Prabhat Chandra Sarbadhikari.

The Treasurer presented his Financial Report and the Accounts of the Society, duly audited, for the year 1937-38.

On a motion by Mr. W. S. ROWNTREE, seconded by Mr. H. R. DARLINGTON, the Report and Statement of Accounts were adopted.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the PRESIDENT declared the Ballot for Council and Officers to be open, and voting began. The Ballot for Council was closed at 5.30 p.m. and for Officers at 6.0 p.m.

Meanwhile the Librarian and Assistant Secretary presented his Report as follows :—

LIST OF THE SOCIETY.—Since the last Anniversary Meeting the Society has lost thirty-five members. The detailed statement is as follows :—

19 FELLOWS BY DEATH :—Edward Thomas Browne, William James Rolph Deeks, Stanley Edwards, William Thomas Elliott, Alfred James Ewart, Sir Cecil Hanbury, Frederick Janson Hanbury, Charles Henry Nicholls, Roger Crompton Notcutt, Frank Armitage Potts, Alfred Barton Rendle, Charles Gilbert Rogers, Lionel Walter The Lord Rothschild, Annie Lorrain Smith, Sir Algernon Phillip Withiel Thomas, Edward Phillips Turner, John Augustus Voelcker, Sir Oscar Emanuel Warburg, Charles Waterfall.

2 FOREIGN MEMBERS BY DEATH.—Richard von Hertwig, Alexander Zahlbruckner.

1 ASSOCIATE BY DEATH :—Richard Francis Towndrow.

9 FELLOWS BY WITHDRAWAL :—James Backhouse, Surendra Chandra Banerji, Edward Hubert Chater, Annie Ethel Cook, Iltyd Buller Pole Evans, Charles Tate Regan, Eva Jennie Savage, Susan Campbell Smith, Joshua Edgar Carrington Turner.

4 FELLOWS BY REMOVAL :—Zafar Alam, Francis Miranda, John Frederick Vicars Phillips, Ram Surat Singh.

During the Session 1 Foreign Member, 2 Associates and 33 Fellows have been elected. Of the 33 Fellows elected, 21 have qualified. 2 Fellows have qualified who were elected during the Session 1936-37.

The present number on the List of Fellows is 726, with 12 Fellows elected, but not yet qualified.

LIBRARY.—Between 1 May 1937 and 30 April 1938 17 books have been purchased and 165 books, 573 parts of periodical publications, and 349 reprints have been presented. During the same period the number of volumes bound was 574. The number of volumes borrowed by Fellows and Associates was 456, and by the National Central Library 193. On the other hand, 23 volumes were borrowed from the Science Library for the use of Fellows. 675 signatures were recorded in the Library Visitors' book, exclusive of 47 for Saturday afternoons.

As in previous years Mr. A. W. Sheppard has given his valuable services as an unofficial worker in the Library.

LINNAEAN COLLECTIONS.—Between 25 May 1937 and 23 May 1938 the collections have been consulted 51 times by visitors: the Herbarium 41 times, 89 genera having been examined; the Zoological collections 10 times. Many other visitors have been given a general view of the Collections. 40 volumes in Linnaeus's Library have been repaired or rebound; in addition many small unbound pamphlets have been collected together in pamphlet boxes.

At the conclusion of this report the PRESIDENT appointed Mr. T. A. Dymes, Mr. H. W. Pugsley and Mr. D. J. Scourfield as Scrutineers of the Ballot.

The PRESIDENT read the text of a telegram to be sent to the Società Botanica Italiana, conveying congratulations on the fiftieth anniversary of the founding of that Society:—

The Linnean Society of London at its 150th Anniversary Meeting sends its greetings and congratulations to the Società Botanica Italiana.

The PRESIDENT addressed the Meeting as follows:—

I have already, in another place, expressed to you my thanks for the high honour you conferred upon me in electing me as your President. I wish here to say that my first satisfaction has been added to by the many kindnesses that I have received from you in my year of office. Owing to the arrangements which have had to be made for holding the Anniversary of the 150th year of our foundation, on a scale which seemed to be expected of us, the year has been a particularly heavy one, and I wish to acknowledge the great amount of work which has been done by the honorary officers and the staff in addition to normal duties of no inconsiderable magnitude. Our Treasurer, moreover, has increased our obligations to him by discharging by a donation the cost

of the celebrations. Your officers are well satisfied with the manner in which Fellows and others have responded to their efforts to make the Celebrations worthy of our honoured traditions. May I say that I hope that the aims and objects of our Society will, by these, be brought to the notice of many who should be amongst us—both amateur and professional. It is probable that few professional biologists are unaware of our activities, but I feel that it is not unlikely that many who are of the type of those who were amongst our first members need the knowledge of our existence and the benefit of our association.

The past year has been heavy in its toll of our ranks. Appropriate obituary notices of our deceased Fellows will be published in our 'Proceedings', and doubtless there some of us will learn for the first time of interests and achievements which we had not suspected. Fortunate in having known most of those who have passed away in my year of office I should have wished to have spoken here of them as I knew them. As it happens, two were my colleagues for many years, but I mention them by name only because of their particular relation to our Society. The one, Miss Annie Lorrain Smith, was of world-wide reputation as a lichenologist, and one of our first six lady fellows. The other, Dr. A. B. Rendle, past President of the Society, formerly Botanical Secretary, was one who served the Society faithfully on its Council and in other ways over a long period.

Fellows will have received during the past week a copy of Col. A. T. Gage's 'A History of the Linnean Society'. I repeat our obligation to Col. Gage for what he has done for us: I know it was a labour of love—but it *was* a labour. We wish him restored health and continued interest in our affairs both past and present.

Our meetings have been well attended, and though perhaps all who partake of tea do not descend afterwards to something more solid, it is a matter of satisfaction that the rooms of the Society should be regarded as a place of social gathering by Fellows and friends of similar interests.

During the recess a new carpet was laid in this room and some improvement made in the seating accommodation regarding both quality and quantity. The expense of these was met out of the Herbert Spencer bequest—and the space for additional seating gained by a slight alteration to the platform, an alteration which takes away somewhat from the comfort of the approach to the five privileged seats, but is, we believe, otherwise wholly advantageous.

The scheme for redecoration which successive Councils have had in view is now completed, and all Fellows will be grateful to the Treasurer for his constant concern for their

comfort. One other arrangement for the convenience of Fellows is the fitting out of a room on the second floor for photographic purposes.

These are the main matters to which your attention may be called. May I end by expressing the hope that the next few days will be profitable to the Society as a whole and to Fellows in particular. In sending our invitations we restricted them to Societies and Institutions at home and abroad which had similar aims to ours. To the delegates of Natural History Societies we would show in every way that we have really the same interests as they have—I know they regard our acknowledgment of their existence as a true and proper patronage—and to our foreign guests that freedom of thought and action which they appreciate as our national birthright, an attitude for universal adoption and a symbol of world peace.

The Scrutineers of the Ballot, who had retired at the appointed times with the voting-lists for the election of the Council and of the Officers, having completed their scrutiny, reported to the President, and he declared the result as follows :—

COUNCIL FOR 1938-39.—Prof. W. A. F. Balfour-Browne ; Dr. B. Barnes ; Mr. I. Henry Burkill ; Mr. R. H. Burne, F.R.S. ; Dr. G. R. de Beer ; Dr. E. Marion Delf ; Capt. Cyril Diver ; Mr. Francis Druce ; Miss M. L. Green ; Dr. Anna B. Hastings ; Mr. M. A. C. Hinton, F.R.S. ; Dr. H. S. Holden ; Mr. Fred Howarth ; Mr. Charles Oldham ; Mr. John Ramsbottom, O.B.E. ; Mr. D. J. Scourfield, I.S.O. ; Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S. ; Dr. Fred Stoker ; Prof. F. E. Weiss, F.R.S. ; Dr. W. H. Wilkins.

(The retiring Councillors are Prof. Eric Ashby, Dr. W. T. Calman, C.B., F.R.S., Dr. Stanley W. Kemp, F.R.S., Mr. A. G. Lowndes, and Dr. E. B. Worthington.)

OFFICERS FOR 1938-39.—*President* : Mr. John Ramsbottom, O.B.E., Dr.Sc. ; *Treasurer* : Mr. Francis Druce ; *Zoological Secretary* : Mr. Martin A. C. Hinton, F.R.S. ; *Botanical Secretary* : Mr. I. Henry Burkill.

The PRESIDENT then announced that he appointed the following as the Vice-Presidents for 1938-39 :—Mr. R. H. Burne, F.R.S., Mr. Francis Druce, Mr. D. J. Scourfield, I.S.O., and Dr. Fred Stoker.

150th ANNIVERSARY CELEBRATIONS, SECOND DAY.

The Society met in open session at 10 a.m. on 25 May in the lecture theatre of The Royal Institution of Great Britain, 21 Albemarle Street.

Mr. J. RAMSBOTTOM, O.B.E., Dr.Sc., President,
in the Chair

The PRESIDENT read the following telegram from ~~His Majesty The King~~ received in reply to the Society's loyal message :—

President,
Linnean Society of London,
Royal Institution,
Albemarle Street, W. 1.

Please convey to the Council and Fellows of The Linnean Society of London the King's sincere thanks for their loyal message. The work which the Society has accomplished for 150 years has contributed greatly to the world's knowledge of the natural sciences, and His Majesty is confident that its great tradition will be maintained in the future.

The following papers, prepared for the symposium, 'The concept of species from the time of Linnaeus to the present day', were then read and were followed by a discussion in which Dr. ERIK STENSÖ, Prof. H. J. LAM, Prof. M. J. SIRKS, Prof. H. BOSCHMA, Prof. B. NĚMEC, Prof. W. ROBŮNS, Dr. W. T. CALMAN, and the PRESIDENT took part; and Prof. Winge replied to Prof. Lam :—

'The conception of species as interbreeding communities.'
By Sir EDWARD B. POULTON, F.R.S. (See pp. 225-6.)

'Mutations and Variations and their bearing on the Origin of Species.' By Prof. E. W. MACBRIDE, F.R.S. (See pp. 227-231.)

'The genetic aspect of the Species Problem.' By Prof. Ø. WINGE. (See pp. 231-238.)

'Palaeontology and the Linnaean Classification.' By Sir ARTHUR SMITH WOODWARD, F.R.S. (See pp. 238-241.)

'The species problem as seen by a systematist.' By Dr. KARL JORDAN, F.R.S. (See pp. 241-247.)

THE CONCEPTION OF SPECIES AS INTERBREEDING COMMUNITIES.

By Sir EDWARD B. POULTON, F.R.S., F.L.S.

I STILL hold the view which I brought before the Entomological Society of London, in an Address * delivered thirty-four years ago—the view that species are interbreeding or syngamic communities, and that this conception is implied in the descriptions drawn up by systematists when these are valid. The proof that a community is syngamic will often be difficult to obtain and long-delayed, but when obtained it will be decisive, and bring release from the necessity of having ‘to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience’—a necessity contemplated by Darwin †, not indeed as ‘a cheering prospect’, but one by which ‘we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species’. The hope expressed in this old Address and my hope to-day is that the conception of species as interbreeding communities supplies this long-sought-for essence.

Continuity or transition of characters between two groups of animals or plants is believed to prove that one is a variety of the other, discontinuity that they are different species. These principles may appear simple, but the subjective element renders their application terribly difficult, as Darwin found when ‡ he wrote to Hooker about the labour expended on Barnacles :—‘I confess I often feel wearied with the work, and cannot help sometimes asking myself what is the good of spending a week or fortnight in ascertaining that certain just perceptible differences blend together, and constitute varieties and not species. As long as I am on anatomy I never feel myself in that disgusting, horrid, *cui bono*, inquiring humour.’

Specific difference inferred from discontinuity, but unconfirmed by the evidence that interbreeding does not occur, has been a fruitful source of error, a striking example being furnished by Hewitson’s criticism of Roland Trimen’s conclusion that certain African butterflies were the females, differing widely from each other, of a male *Papilio* still more different from all of them : and it was finally the evidence brought by his own collector who had caught a male paired

* ‘What is a Species?’, read at the Annual Meeting on 20 January 1904.

† ‘The Origin of Species’, 1st ed. 1859, p. 485.

‡ ‘Life and Letters of Charles Darwin’, 1887, I, p. 379.

with one of these females which convinced him that 'the childish guesses of the Darwinian school', as he had called them, were well-founded conclusions*.

The splendid collection made by the late Lord Rothschild, and left by him to the Nation, has been the leading influence in bringing before the world the conception of subspecific groups still fused by syngamy into single species, but ever ready, by preferential mating or the effects of isolation, to break up into separate species. A museum following the great example of Tring becomes an inspiring centre of research in the spirit of Dr. Karl Jordan's words published in its Journal†:—'The actual proof of specific distinctness the systematist as such cannot bring; . . . we work, or we ought to work, with the mental reservation that the specific distinctness of our *species novae* deduced from morphological differences will be corroborated by biology.'

The conception of species here briefly summarized has received firm support from the researches of geneticists, enabling us to understand the readiness with which a single community may break up into two or more communities as the effect of Mendelian combinations upon the germinal basis of intersexual congruity. Do not these researches suggest a means by which the infinitely delicate balance may be upset by isolation, leading to the cessation of interbreeding, either directly, or indirectly by changes in the material basis of intersexual recognition and attraction?

Dobzhansky, in his recent work on 'Genetics and the Origin of Species', adopts the conception of a syngamic community of which the origin is defined as 'that stage of the evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding'. Prof. A. E. Emerson, in reviewing the above-mentioned work ‡, quotes a definition which for several years he has been accustomed to use in teaching:—'A species is a genetically distinctive, reproductively isolated, natural population.'

In conclusion, I venture to re-affirm my belief in the conception of species as an interbreeding community, and in its confirmation by Mendelian research.

* *Trans. Entom. Soc. Lond.* 1874, p. 137; also *Entom. Monthly Mag.*, Oct. 1874, p. 113.

† *Novitates Zoologicae*, III, Dec. 1896, pp. 450, 451.

‡ *Ecology*, XIX, No. 1, Jan. 1938, p. 153.

MUTATIONS AND VARIATIONS AND THEIR BEARING ON THE ORIGIN OF SPECIES.

By Professor E. W. MACBRIDE, F.R.S., F.L.S.

I WAS in some doubt when I came here as to what my part and order in the discussion would be. Intimation of the aspect from which I was expected to speak was contained in the single line I received some time ago, namely, 'Mutations and Varieties'. I agree with a great deal that my predecessor, Sir Edward Poulton, has said. The old idea that species were created by the Almighty, an idea which was advocated all his life by Cuvier, has, of course, passed into the limbo of forgotten things. If they were not so created then they must be natural growths, and there is no escape from Darwin's conclusion that the terms 'species' and 'varieties' grade into one another. In fact, I think that the first three chapters of Darwin's immortal book on the *Origin of Species* constitute the essence of the whole subject and contain also one of the three great proofs that evolution really did take place. For if it is not possible to draw the line between variety and species, still less can it be drawn between species and genus. In fact, the modern systematists, my friends of the British Museum, know only too well that every authority quarrels with every other as to the number of genera, and we are torn between what are called 'the lumpers' and 'the splitters'.

Speaking for myself, I am a lumper. My favourite group, and the one to which I have devoted a great deal of study during my life, the Echinodermata, is changed out of all recognition by the splitters. When papers announce the reaction of *Marthasterias*, for instance, to various reagents I wonder what on earth I am reading about, and then it dawns upon me it is the old *Asterias glacialis*. No one could tell that from the title. When I hear mention of *Parechinus*, *Psamm-echinus* and such things, it may well be realized that I am listening to the old story of the sea-urchin, *Echinus microtuberculatus*.

The question of the whole evolution of life narrows itself down to what is the nature of the differences that separate individuals from one another. It is on that I wish to say a few words.

One of the great discoveries made in, say, the last forty years was that these individual differences on which Darwin laid so much stress—he thought it was out of them that species had, so to speak, been constructed—are not heritable. They can have had no part whatever in the formation of species. That has been proved by the pure-line investigations carried out by Johannsen in the bean-plant, by Agar in the little

crustacean, *Simocephalus* (sometimes called *Daphne*), and by Jennings with the protozoan, *Paramoecium*.

If, then, these individual differences are ruled out, can we fall back on mutations? That is the suggestion that is still held firmly by a good many workers. I am a member of the John Innes Horticultural Institution, on the Council of which I have had the honour of serving for twenty-five years. You will find there a number of people who are as obstinate in holding to the belief that mutations are the basis of the origin of species as a pious Catholic is of the Immaculate Conception of the Virgin Mary. They cannot see that there is no proof whatever that mutations have had anything to do with the formation of species.

On the contrary, mutations, whenever they have been artificially made, as in recent years, by the action of X-rays and by the action of heat, have proved to be pathologically deranged specimens, and as such they would have no possible chance of survival in the battle for life. Nay, more: when these mutations succeed in colonizing some Eden in which their natural enemies do not exist they revert to the wild ancestry, showing that the whole potency of that wild ancestry persists underneath the superficial disturbance.

As most of you know, the best instance of that is the domestic pig in New Zealand. My colleague and friend, Lord Onslow, who is now President of the Zoological Society, in his youth lived in New Zealand when his father was Governor of that Dominion, and he was greatly interested in the field-pig. The history is entertaining. It appears that when Captain Cook first visited New Zealand he found the gentle Maori in the habit of feasting on their young girls or superfluous women. In order to wean the Maori from this habit Captain Cook thought he would introduce the pig. He accordingly brought over a number of the New Forest variety, and when he gave them to the Maori chiefs he told them how the pigs were to be looked after. The Maoris, however, had no idea of husbandry, and small blame to them, for in New Zealand there was nothing to husband. There were no mammals; consequently, what was the use of being a cattle farmer? So the pigs were allowed to escape into the bush, and forty years later they had completely reverted to the wild boar—so completely indeed, that they were a menace to the sheep flocks of the English colonists, or, more correctly, the Scottish colonists who in the meantime arrived.

Lord Onslow gave me a tusk of one of these feral pigs, so long that it would have done credit to any wild boar. You may say that I cannot refer to the same happening elsewhere. Naturally, because in Natural History we must select for examination the case where the circumstances can be minutely

observed and brought under control. I think the instance of the pigs deals the final blow to the theory that mutations can have had anything to do with species.

I have jotted down two or three sentences from de Vries, who, as you know, introduced the word 'mutation'. He said: 'Mutations are chance phenomena into whose essential nature we have no insight. They consist in the loss or latency of a character. So-called rogues are merely hybrids, and improvement is generally complete in five generations. Thus Vilmorin made the wild carrot into the typical rich fleshy carrot in five generations.' There you see what mutations are.

Sir Edward Poulton alluded, but very gently, to the theory that by examination of the germ-cell it is possible to find out something as to the mechanism of how these variations etc. occur. I went into that question in some detail about a year ago, and I came to the conclusion that the whole Morgan theory of chromosomes was a castle of cards built on an insecure basis. It all goes back to the idea that when the essential parts of the nuclei, the male and female, go together long male and female chromosomes lie side by side, as it were kissing each other; and Morgan assumed, though he never could demonstrate it, that pieces of one chromosome broke off, crossed over and joined the other chromosome, and this was supposed to be the basis of mutation.

When that theory came to be looked into, first under the distinguished auspices of Professor Graham Kerr, under whose supervision the actual observations were carried out by his pupil, Professor Agar, and, secondly, by Walker of Liverpool, who examined it in more detail, the apparent kissing of two chromosomes, one male and one female, proved to be the first division of the chromosomes. After they had divided and the nucleus had proceeded with its maturation it was possible to see the real touching or meiosis of the chromosomes, but by that time the chromosomes had been reduced to little round knobs or spheroids, and by no conceivable stretch of the imagination would anyone imagine that little things like these could break into thin pieces and exchange such pieces with one another.

So that if the fluctuating variations are not heritable, and if mutations are found to be due to secondary interference with the ingrained characters of the germ, how did one species gradually change into another? I suppose most of you know the answer that I am prepared to give. I hold that what was guessed by Lamarck, and the conclusion independently arrived at by my very distinguished friend Mr. Hinton, Keeper of Zoology in the Natural History Museum, that reaction to changed circumstances, change of habit, etc., becomes slowly

ingrained, and eventually after a long time gives rise to species—I hold that that guess and that conclusion have now passed from the region of hypothesis to the region of fact.

I am having printed at the Royal Society the consummation of the last work of my dear pupil, Miss Dorothy Sladden, who was killed in a motor accident about two years ago. My former colleague, Mr. Hewer, has been gathering up her work and putting down the results, and it is shown most conclusively that if an animal is forced to take food which it does not like and the forcing is continuous, at first the animal has to be forced for long before it will accept the food. As generations succeed one another the animal takes the disliked food more readily, until, after about five or six generations, 100 per cent. of the particular group of animal take it at the first chance. That is, one might say, the coping-stone in the proof; but that proof only corroborates the conclusion that McDougall, one of our most distinguished Cambridge professors, came to with regard to rats. I have not time to take you through the experiments he conducted with rats when teaching them that if they persisted in going in a certain way to a platform that they wanted to get on to they would get a shock. He showed that after two or three generations had been shocked the animal came to learn what was coming to it after a very slight indication, which could not be put down to a warning from the mother. Incidentally, long experience with animals has taught me that it is a great mistake to under-rate their intelligence. McDougall found that if he took the young rats at birth and put them under a foster-mother who had not been through the terrifying experience the effort to avoid the shock showed itself just as quickly. So that I think we have now arrived at the final proof that habit is a driving force of evolution, and that it is slow change of habit that produces species.

Those who on various grounds dislike this conclusion naturally say: That is all very plausible, but if that were the case would not we find that it is far more flexible than the use already being made of it? A distinguished German professor, a friend of mine, Professor Woltreck, has succeeded in answering that question. He described how in Bavaria in South Germany he found a region which had been overflowed by a great Alpine glacier which had its origin in the icefield in the central Alps. When the glacier commenced to recede as the climate grew milder it left exposed, naturally, a lot of boulder-clay. In that clay there were glacial lakes. If he examined the minute Crustacea in those lakes, and compared them with their nearest allies in the lakes outside the limit of the moraine, he was able to detect differences, but differences which, though constant, were so slight that he declined to dignify the new

form with the name of a species : he called it a variety or a race. The estimate of the time since that glacier commenced to recede is about 16,000 years. Now, if it takes 16,000 years to produce a new race, you can imagine the time and scale on which it is our duty to calculate the origin of species.

THE GENETIC ASPECT OF THE SPECIES PROBLEM.

By Professor Ø. WINGE,
The Carlsberg Laboratory, Copenhagen.

WE all know that differences between two allied species are of a genetic nature. This is beyond any discussion. The problem, however, presents several difficulties as soon as the question arises how to determine the differences in genetic terms, such as : how great the difference is, how many genes are involved, and whether possibly not only the nucleus, but the cytoplasm too, is of specific characterizing nature.

The usual technique in determining the genetic difference between any two types under consideration consists in crossing these and in determining, through a study of the hybrid and its progeny, which and how many genes are different in the two types. In hybridizing two varieties within the same Linnaean species the number of genes involved is often rather limited. Sometimes two varieties differ in one gene only, and the progeny of their hybrid show a simple Mendelian ratio. Numerous analyses of this category are available in the literature.

Species-differences are more difficult to analyse, as very frequently it is difficult to hybridize different species, or if the cross is successfully produced the hybrid shows part or complete sterility, thus blocking the way for analysis. Exceptions exist, however. Some species-hybrids are completely fertile, a fact that has given rise to considerations whether the distinction of the parental types as different species was justified. We need only think of the two Linnaean species of peas, *Pisum arvense* and *P. sativum*. The two species have the same chromosome number. Their hybrid is completely fertile, and the progeny show Mendelian ratios demonstrating a limited number of genes involved. From a genetic point of view these two types are not specifically different, and, moreover, taxonomists seem recently inclined to regard them as two varieties of the same species.

On the other hand, the interpretation of *Lychnis dioica* Linn. appears to have changed in the opposite direction. Taxonomists nowadays regard *Melandrium rubrum* and

M. album generally as two well-defined species, though Linné considered them as two varieties, α and β , of *Lychnis dioica*. Genetic experiments show that the hybrid is fully fertile, and its progeny exhibits normal though rather complicated segregations. Geneticists will be inclined to regard these two types as belonging to the same species, a view confirmed by the cytologists. Both species have twelve chromosomes, one set being sex chromosomes, and the chromosomes conjugate regularly in the hybrid.

From a cyto-genetical point of view, a third instance of an ambiguous classification is *Geum rivale* and *G. urbanum*. Both species were described by Linné, and they have undoubtedly always been considered well-defined species. Genetically, however, this instance closely resembles the two before-mentioned. Crossing experiments and cytological studies lead to the conclusion that these two types are merely varieties of one species. Taxonomists, on the other hand, will undoubtedly claim a specific distinction between the types, as the latter, e.g., have different ecological requirements.

An interesting problem arises particularly in the last-mentioned instance. *Geum rivale* and *G. urbanum* have practically the same area of distribution. They hybridize frequently in Nature and the hybrid is fertile. Nevertheless, they appear always well separated. In reality several individuals, apparently pure types of the one species, contain undoubtedly some 'blood' from the other species. I had, some years ago, five large F_2 generations (about 2,000 plants) from the selfing of five F_1 individuals of different origin. It was evident that amongst the five different F_2 generations some on the whole resembled more *rivale*, others more *urbanum*. This was undoubtedly due to the fact that the individuals of the pure species used in hybridization were not identical. In reality I think they contained different numbers of genes from the other species as a result of a previous accidental crossing. The possibility seems to exist, in such instances, that two species, as those just mentioned, may in thousands of years approach one another and perhaps finally be merged into one species.

These may be taken as examples of taxonomists being inclined to recognize a species distinction, where cyto-geneticists would rather claim mere variety differences.

The opposite phenomenon exists, too. I shall confine myself to one instance only, which I have had particular opportunity to work on for many years.

Taxonomists have a species described by Linné as *Draba verna*. It is now known as *Erophila verna*. It is a small insignificant cruciferous spring flower with small white petals. Taxonomists recognize it as a well-defined Linnaean species, although it includes several varieties.

A cytological study of the *Erophila verna* types in Nature shows a whole series of different chromosome numbers, and by practice it is easy to identify some of the types with absolute certainty. The lowest chromosome number is 7. This type is very frequent—perhaps the most frequent—in Denmark, while so far I have not observed it either in England or in Scotland. The seven-chromosomed type is easy to distinguish from all others as being always characteristic of the same morphological phenotype. Types are known with 12 chromosomes (so far from Germany only). 15 is a very common number, perhaps the most frequent in *Erophila*. Other types have 17, 18, 19, 22, 26, 29, and 32 chromosomes, but they are more difficult to distinguish.

Hybrids between types with different chromosome numbers such as 7×32 are sterile. Several other hybrids, too, are more or less sterile.

Cytogenetically there is no doubt that Nature recognizes these different types of *Erophila* as specifically different. Taxonomists combine all the types in one species, as they are very difficult or even impossible to distinguish in Nature, though their characteristic differences are easily observed when they are cultivated in seed-boxes under similar greenhouse conditions. I feel strongly convinced that if *Erophila* had been three feet instead of three inches high, the differences would show up sufficiently impressively, and no taxonomist would think of combining, e.g., the seven-chromosomed type with any of the other types.

These circumstances show that the species conception of the taxonomists is of a *practical* nature. Types indistinguishable in Nature by the naked eye and a lens are reckoned as the same species even if they are clearly separable biologically and cytologically. The taxonomist and the museums cannot undertake cultivation, perhaps hybridizing, and cytological studies of a material in order to determine a species.

Consequently it is quite natural that a universally recognized definition of species does not exist. A geneticist would define the species conception by expressing the *species difference* somewhat as follows: *individuals are specifically different when they are either unable to hybridize or when, by crossing, they produce more or less sterile progeny.*

This definition is not quite ideal, however, as some well-defined species show 'incompatibility', that is, some types within the species are unable to fertilize one another: and, furthermore, pure Linnaean species *may* show sterility due to either sterility genes or chromosome abnormalities.

But even disregarding the exceptions taxonomists would scarcely adopt the species definition of the geneticist. And even so difficulties would still appear, as intermediate forms would exist in spite of all definitions.

The geneticist may in some instances supply to the taxonomist hints as to the extent of differences between any two given types, but he cannot interfere with the taxonomist whose attitude, as already mentioned, must be more practical.

The geneticist may feel impelled to exercise his influence on one point, viz., with regard to the apogamous species of plants (Agamospecies). The countless types already described as species and still being described within such genera as *Hieracium* and *Taraxacum* appear rather pointless and a wasting of print and paper. It is evident that every new mutant is constant and that the number of clones is unlimited within these genera. It is too much like the collecting of stamps to sort out all the clones in Nature within such a species as *Taraxacum vulgare*. They generally show no ecological differences. It seems that the phanerogamists here lay too much stress on immaterial bagatelles.

The cyto-geneticist finds a peculiar difficulty in the species conception with regard to the polyploid types which are particularly frequent in plants. What is to be done, e.g., with *Narcissus Bulbocodium*, which appears in Nature with 14, 21, 28, 35, and 42 somatic chromosomes (Fernandes), or with *Potentilla argentea*, which is now diploid with $2n=14$, now hexaploid with 42, or octoploid with 56 (Müntzing). Such types with different chromosome numbers exhibit frequently a higher or lower degree of sterility in reciprocal hybridization, but scarcely anybody would think of designating them as different species. They are types of different atomicity, if I may be allowed an analogy with chemistry where, e.g., sulphur appears with the valence of 2, 4, or 6.

These types are expressions of the fact that the species is never static, and that evolution is always taking place. Polyploid types, so far, have not involved greater difficulties in taxonomy, and they will not do so in future either. The knowledge of these, however, is of considerable value to the understanding of evolution in Nature.

Other experiences of late years have shown that genes may be located differently in the chromosomes of the same species. Dobzhansky and Sturtevant in a paper of this year have established numerous *inversions* of chromosome parts in the wild-type of *Drosophila pseudo-obscura*. Different geographical races with characteristic gene-topography exist, but different types may be found in the same locality. Also in such a plant as *Datura Stramonium*, Blakeslee and collaborators find even considerable *translocations*, i.e., interchanges between different chromosomes, in a long series of wild-growing types. But even though this is of the greatest importance to the understanding of evolution, it will hardly seriously affect the daily work and interest of the taxonomists.

In the introduction to this address I have touched on the question whether (1) the difference between recognized Linnaean species is to be found in the nucleus alone (in other words, in a certain number of gene differences in the chromosomes) or whether (2) the cytoplasm too is of a species-characterizing nature.

From numerous experimental results in hand we know that in higher plants the cytoplasm *can* contain genetic peculiarities, particularly such as concern chlorophyll qualities. But so far this does not tell us whether in two allied species it is a *characteristic* that their cytoplasm is genetically different.

W. Johannsen, the late Danish geneticist, often expressed a doubt whether the factors analysed in the segregation of a hybrid were after all of significant character. He believed that Mendelian characters were of a rather insignificant nature and that the analysis did not produce any information about the behaviour of the more fundamental genes. Johannsen was also doubtful as to the question whether *mutations* caused profound changes of a fundamental nature. He claimed, rightly, that even if the fruit-fly, *Drosophila melanogaster*, passed through ever so many mutations it would still remain a fruit-fly.

In other words, to Johannsen it was questionable whether the taxonomically fundamental characters were due to ordinary genes located in the chromosomes—or whether the essential substance did not leaven the organism as a whole and perhaps particularly the cytoplasm.

We have been more and more convinced, however, by the experiments of later years that species differences are essentially due to gene differences in the chromosomes, and that Johannsen's doubt was gratuitous.

Navashin's experiments (1927) with the hybrid *Crepis setosa* × *C. capillaris* showed that it was possible in each individual of the progeny cytologically to demonstrate from which of the parental species each chromosome originated. A segregated type, containing exclusively the chromosomes of one species with the cytoplasm of the other species (transmitted through the ovule), is completely like the species yielding the chromosomes. The cytoplasm has no influence.

Hämmerling's experiments with the green alga *Acetabularia* (1934 and 1936) in the same manner show that the nucleus alone is the vital factor in the development of an individual.

During a number of years I have made experiments with different species-hybrids in order to investigate the genetic difference between recognized Linnaean species.

Thus, I have crossed the two species *Tragopogon pratensis* and *T. porrifolius*. In spite of both species having six chromosomes F_1 is almost sterile, but the chromosomes are slightly

different in the two species. It is, however, possible to obtain some F_2 individuals. Both the pure *Tragopogon* species were successfully segregated out in the selection within F_2 and their progeny through several generations. No taxonomist would be able to ascertain that these two specific pure types, segregates from the hybrid, had ever been involved in a cross. It is not merely a superficial similarity between the original and the segregated pure species; for all details in growth, flower-colour, shape, and size of the fruits etc. agree. The two segregated pure types were cytologically in conformity with the original parental types. A paper dealing with this cross has just appeared.

Similar observations have been made in the hybrid *Verbena tenera* $\times$ *V. Aubletia*. Studies, carried on through more than fifteen years, show that the hybrid between the two species is capable of segregating out the pure parental species. These studies are still unpublished.

These examples show that no genetically fundamental difference need exist between the cytoplasm in two distinct Linnaean species. Otherwise it would not have been possible to get both parental species segregated out. *The species difference depends on chromosome differences, i.e. on segregating gene-differences in chromosomes.*

The species, as realized in Nature, represents a gene-combination involving a particularly well-balanced physiology in the type.

But how are we to imagine a genetic difference between two species belonging for instance to quite different genera or even families?

Fifteen years ago I put forward my point of view based in particular on the cyto-taxonomical considerations: that chromosome doubling produces new species of plants, and that chromosome conjugations take place (to which might now be added duplications and translocations). All these factors would result in 'a gradual, manifold appearance of the same factors in each single chromosome or, in any case, in more than one'.

These considerations led to the conclusion that the larger the systematic unit under consideration, the more often must the genes, characteristic of that unit, be repeated in the chromosomes and probably even in all the chromosomes.

'As two varieties, chosen within a species, only differ as far as a few factors, the "variety-factors", are concerned, but are homozygotic and isogenous with regard to all the species-, genus-, family-, etc. factors, the effect of variety-factors is alone observed in segregations.'

'Of course, one could not think of any absolute boundary between, for instance, "species-factors" and "variety-factors";

but we must suppose that, in substance, those factors which are widely represented in all the chromosomes afford a basis for classification into large taxonomic units; their frequent presence in the chromosomes will entirely prevent a segregation into types in which these factors are lacking, and the loss or the modification of a few such factors could hardly provoke any immediately visible mutation, because many others of the same nature would be left. At the most, this eventuality could be imagined to tend, throughout a long period of time, towards a slow shift in the characters of the species—a condition of things which might be associated with biological evolution'.

This hypothesis, put forward in 1923, may be called *the hypothesis of the taxonomic importance of polymery*, a hypothesis supported mainly by observations in plants and without much evidence from studies in animals.

In the present state of knowledge it is impossible to exclude other hypotheses of the nature of taxonomically important genes.

Are, then, lethal genes the most important taxonomically? The normal alleles of 'lethal genes', i.e. 'vital genes', are necessary for the existence of an individual, thus indicating that they are a very important part of the nature of species and that these genes are characteristic of species, genera, and families.

The knowledge of the morphological expression of lethal genes somewhat bears out *this hypothesis of the taxonomic importance of the alleles to lethal genes*. The morphological species-characters exhibiting Mendelian ratios, e.g., in the *Tragopogon* cross would in consequence be accessory phenomena only, and the genes under observation are merely linked to those genes characteristic of species which are of more fundamental significance. In the present state of knowledge this hypothesis may scarcely be rejected.

A third hypothesis has to be taken into consideration, too. Studies in mutations have shown that genes exhibit all gradations of stability. Certain genes are quite unstable, whereas others are very stable. Genes mutating only to their recessives appear to be more frequent than those mutating in both directions with even frequencies.

Species characters (respectively genera and family characters) are the most stable. This *may* signify that the constancy of these characters is due to a particular stable nature of the genes in question. This *hypothesis of the stability of genes of taxonomic importance* may be the object of studies simultaneously with the increasing knowledge of mutation frequencies. Sufficient material for a study of mutation frequencies in different genes is probably not available as yet—not even in

Drosophila. Are the majority of mutable genes extremely stable, are a smaller number of intermediate stability, and are a few unstable? Or are the majority of genes of intermediate stability and the numbers decreasing both in the direction of more stable and of unstable genes? Or how is the distribution? In the present state of knowledge the arrangement first mentioned appears more probable. This would imply the presence of a large number of almost completely stable genes escaping analysis on account of their stability. These genes, then, most probably would be of the greatest taxonomic importance.

A study of the problems in question will be of great interest. So far, we only know that differences between species depend on differences in genes which are located in the chromosomes and consequently exhibiting Mendelian ratios.

Hybridization experiments have failed in disclosing whether all genes are of the same taxonomic importance or whether certain genes are particularly significant as I have indicated. This remains a problem for future studies.

PALAEONTOLOGY AND THE LINNAEAN CLASSIFICATION.

BY SIR ARTHUR SMITH WOODWARD, F.R.S., F.L.S.

THOSE who are interested in systematic zoology have realized for some time that our increasing knowledge of extinct animals makes the use of the Linnaean method of classification very difficult. We are beginning to learn that we cannot arrange animals according to their natural affinities if we are restricted like Linnaeus, to those living together at one period of time. We can only make satisfactory classifications when fossils enable us to trace the ancestors of the various groups through a series of geological epochs. Instead of classes, orders, families, and genera, we are concerned with phyla, lineages, branches, and grades; and we soon discover that related lineages pass through the same orderly succession of changes by which the same—or nearly the same—result is eventually attained. This means that when we are dealing only with existing animals or the associated animals of any single geological period, the families and genera, at least, which we establish consist of members that are not so closely related as they seem to be. They are merely the end shoots of a series of parallel lineages which have reached the same grade of development.

Take as a simple illustration the oft-quoted evolution of the Graptolites which lived in all seas during the early Palaeozoic periods. When they first appeared, the little rods bearing the row of cells which were occupied by the polyps

formed a more or less complicated network. Somewhat later in geological time very few networks were left, and most of the Graptolite colonies were irregularly branched. Still later, most Graptolites were characterized by only four branches. Next there appeared the 'tuning-fork' Graptolites and other forms with only one pair of branches. Finally, just before their extinction, all Graptolites were simplified into single unbranched rods. The study of the polyp-cells and other characters shows that during the successive geological periods there were several distinct lineages among the Graptolites which passed from grade to grade in this definite way. To classify them in related groups, therefore, we must try to follow the lineages, and not be satisfied with the old names *Tetragraptus*, *Didymograptus*, *Monograptus*, and so on, which were originally given to them before the succession of grades had been recognized.

Many other known illustrations among the invertebrates might be cited, and there are now also still more striking examples of parallel development in the lineages even of the highest vertebrates. The late Professor H. F. Osborn among others observed several parallel lineages of horses, rhinoceroses, elephants, camels, and some extinct groups of mammals, and the difficulty of arranging these on the Linnaean plan may be realized by scanning the pages of the English edition of Zittel's 'Text-book of Palaeontology', vol. III (1925), which was based partly on his work.

The latest researches seem to show that, if skeletons correctly indicate the nature of the soft parts, the successive great groups or grades have also arisen from more than one source. Among fishes, for example, the ordinary Elasmobranchs, with no true bone and a dermal skeleton of dentine, may comprise lineages from one ancestral stock; but just before they began to appear in the form of *Pleuropterygii* (*Cladospelache*, etc.) towards the end of the Devonian period, there were also other Elasmobranchs with an armour of plates which consisted of peculiar laminated bone and scarcely any dentine. *Gemuendina**, from the Lower Devonian of Rhenish Prussia and *Macropetalichthys*†, both from this and later Devonian formations, are the best-known examples. They almost lost their dermal armour before they disappeared, as shown by *Cratospelache*‡ from the Lower Carboniferous of Belgium. These early armoured Elasmobranchs, or *Stegoselachii*, bore so many resemblances to the contemporary

* F. Broili, Abhandl. Bayer. Akad. Wiss., Math.-naturwiss. Abt., n.F., no. 6 (1930), pp. 1-24; also Sitzungsber. Bayer. Akad. Wiss., Math.-naturwiss. Abt., 1933, pp. 269-281.

† F. Broili, Sitzungsber. Bayer. Akad. Wiss., Math.-naturwiss. Abt., 1933, pp. 417-437.

‡ A. S. Woodward, Livre Jubilaire Soc. Géol. Belg., 1924, pp. 59-64.

Arthrodiran fishes that they may have had common ancestors. There is not much doubt, therefore, that Elasmobranch fishes arose in at least two distinct lineages.

Recent discoveries in the Lower Triassic formations of Australia, South Africa, Madagascar, and East Greenland have also shown that the primitive Chondrosteian Ganoids passed into the next higher grade, that of the Protospondyli, in more than one lineage. It has long been known that the generalized fusiform Chondrosteans of the family Palæoniscidæ pass by gradual stages through the Triassic Catopteridæ into the Protospondylic grade which flourished especially later. It now appears * that even such specialized Palæozoic Chondrosteans as the Platysomidæ and their allies advanced directly towards the Protospondylic grade, and may have been the immediate ancestors of the Mesozoic Pycnodontidæ.

Similarly, it is difficult to explain the early differentiation of the modern teleostean fishes, except by supposing that they originated independently from several lineages of the Ganoids which preceded them. Such highly specialized fishes as the eels, for example, were already distinct in the Upper Cretaceous, and typical Siluroids were varied even at the beginning of the Tertiary; nevertheless, no generalized Teleosteans from which they could have been derived are known from earlier geological formations.

The Amphibia seem to have first appeared in the Devonian period when the dominant fishes, the Crossopterygii and Dipnoi, made the nearest approach to them; but the links between these two grades are still not clearly recognized. The early Amphibia, however, pass into the earliest Reptilia through at least three distinct lineages. Certain small lizard-shaped quadrupeds of the Permo-Carboniferous period, such as *Sauravus* †, are sometimes claimed to be amphibians, sometimes reptiles; while the comparatively large and massive Seymouriidæ ‡, of the Permian period, are so completely on the border-line that they have led to much inconclusive discussion. Quite lately, Baron F. von Huene § has also shown that the Ichthyosauria must be the direct descendants of an early group of Amphibia, the Embolomerous Stegocephalians.

Birds and Mammals also appear to have been derived

* E. I. White, *Ann. & Mag. Nat. Hist.* [10] x (1932), pp. 80-83; E. A. Stensiö, *Medd. om Grönland*, LXXXIII, no. 3 (1932), pp. 125-164 (*Bobasatraniidae*).

† A. Thevenin, *Annales paléont.*, v (1910), pp. 43-46; S. W. Williston, *Journ. Geol.*, xvi (1908), pp. 395-400.

‡ A. S. Romer, *Journ. Geol.*, xxxvi (1928), pp. 248-260.

§ F. von Huene, *Bull. Geol. Inst. Upsala*, xxvii (1937), pp. 1-9.

respectively from more than one source, but many more fossils are needed before the evidence is clear.

Palaeontologists are therefore tempted to discard the Linnaean system of nomenclature, and some of them have actually tried to invent new principles for naming both species, genera, and the larger groups. I think, however, the effort is premature, and it is more convenient to retain the old system as a provisional expedient until further studies of fossils make us more sure of our facts.

THE SPECIES PROBLEM AS SEEN BY A SYSTEMATIST.

BY DR. KARL JORDAN, F.R.S.

HAVING listened with great interest to the exposition of the species concept in botany, I realize that the zoological and botanical concepts of what constitutes a species are not quite the same. The so-called small species which exist side by side in plants have no actual homologon in animals, and, while fertilization is a more or less mechanical process in plants, a preliminary physiological or psychological factor comes largely into play among animals. The transmission of the pollen being to a considerable extent achieved by the external agencies of wind and insects, mistakes often occur; hybridization is frequent, and hybrid strains often persist. In animals, on the other hand, the sexes of the same species are adapted to and attracted by each other and have an aversion towards the opposite sex of other species, the purity of the species being thereby safeguarded and hybridization rare under normal conditions. The question of interbreeding and the absence or reduction of fertility in hybrids is of the greatest importance in the species concept in zoology, and less so in botany.

Speaking as a zoologist who has spent the larger part of his life battling in a museum with the species problem in its great variety, I propose to confine in this discussion my contribution to some aspects of the subject which have continually forced themselves on our notice in studying the systematics of particular groups of animals, especially my own entomological specialities. Some forty years ago Dr. A. G. Butler, the Keeper of Entomology in the British Museum, in showing me two specimens of African butterflies, put this problem to me: 'As you see, he said, the specimens are similar to each other, but differ from all the others we have in the collection; I maintain, therefore, that they are a different species and, nothing like them being described, a new species. Jones does not agree, and I have told him that it is up to him

to prove I am wrong.' Now, what is it that Jones would have to prove and how could it be proved? If you look closely at Butler's statement of this case, you will detect a serious flaw in it. He referred to the two specimens as a species. They were nothing of the kind, but examples of a species. If Butler's expression is taken as a mere figure of speech, it is harmless; but if it is used in its literal sense in an argument, the issue is much confused. The difference is fundamental; in a discussion of the species concept we must clear our mind of the notion that a specimen is the same as a species. Our collections do not contain the species, but specimens of them. From spring to autumn our gardens teem with animal life which makes itself conspicuous by song, colour, or the damage inflicted on our precious plants; there are blackbird, song-thrush, robin, orange-tip butterfly, green-flies on the roses, the slugs and snails, pet aversions of the gardener, and a multitude of others that make the gardens their home in all districts of Great Britain. When we wish to refer to the aggregate of the human beings inhabiting these isles, we speak of the human population, the term comprising all individuals, however different they may be in their somatic and psychological make-up. Similarly, we must conceive all the individual bank-voles of Great Britain as the bank-vole population, the orange-tips as the orange-tip population, and so on, each specific population comprising every specimen of generation after generation, however peculiar it may be in appearance or behaviour. In a fair-sized garden hundreds of such populations are represented, in Great Britain many thousands, and on the whole globe millions. The specific populations, some of which may be very similar to each other, are not kept apart as independent units by any extraneous barrier, but by their own specificity. This non-amalgamation is the criterion of specific distinction in any given place, each species being an interbreeding community, as Sir Edward Poulton has explained. Even if their physiological constitution does not prevent two species from interbreeding, as for instance in the case of ducks or in the cramped space of an oasis, the hybridization has no lasting effect on the species as a whole.

All research in systematics proceeds from the comparison of individual specimens; the correctness of the separation of the specimens into species depends on the knowledge of the latitude of variability in the populations concerned, and this knowledge must be acquired by research on material of which we are sure by observation or by breeding that it is pure, i.e. that the specimens stand to each other in the relation of brothers and sisters of known pure parentage, or of pure parents and offspring. The first important result of such an enquiry is the fact that no two individuals are ever identical,

however similar they may be ; every one has its own peculiarities, like the sheep of a flock. And we find further that the differences between individuals, the sexes, the generations are often so considerable that they have frequently been mistaken for specific or even generic distinctions. But how can we possibly ascertain the limits of variability of any specific populations, considering that areas inhabited are large and the numbers of specimens of generation after generation enormous? Here the enthusiastic amateur specialists come to the rescue by collecting, observing, and breeding, at least in all such groups which lend themselves to the making of private collections. Considered from this point of view, the collecting of aberrant specimens, so often looked upon as a pastime similar to stamp-collecting, assumes a different aspect, and should be encouraged. Nevertheless, even in Europe, the larger number of specific populations are but imperfectly known. It seems too much to hope for a well-organized survey of the fauna of Western Europe, the U.S.S.R. being in advance of us in that respect, at least as regards the rodent populations and their parasites. As an example of the great services rendered to systematics by a naturalist, non-professional at that time, I mention that just forty years ago Sir Guy Marshall proved by breeding that two African butterflies, very different in colour and wing-shape, and till then always treated as two distinct species not very nearly related to each other, were in fact nothing but the wet and dry season forms of one species. This astonishing discovery was disconcerting, and Butler very wisely reversed his argument altogether. It was made too plain that differences are not necessarily specific ; he went to the other extreme and became a lumpner, as it is rather inelegantly called, and there remained nothing for Jones to prove.

As regards the fauna of the tropics and other insufficiently explored countries, the number of specific populations represented in collections by haphazard examples is appallingly large. The systematist is constantly hampered in his research by this inadequacy of the material at hand, as we know only too well from experience at Tring ; the conclusions derived from such material are provisional ; they hang in the air until further material confirms or refutes them. This consideration induced Lord Rothschild to insist on acquiring large series, maintaining that the number of specimens available for research could never be too large. There are in consequence at Tring species of Lepidoptera represented by thousands of specimens, and it was Lord Rothschild's wish, expressed in the Codicil to his Will, that this material should remain available for research and not be scattered or otherwise destroyed. It is obvious that the more extensive is the

material of a species from a certain area in a museum, the greater is the chance that it represents approximately the latitude of variability of the species in that place.

Fortunately for the systematist, the somatics of a species do not all vary to the same extent, co-ordination in the different organs being rare, and he learns from experience in which organs of the particular group of animals he is studying the variability is confined to narrow limits, so that these organs can be safely taken as guides in distinguishing one species from the other. In insects the accessory genital organs are of this nature, and their study, particularly in moths, is often the only means of recognizing a species, and their description is as necessary in Lepidoptera as is that of the skull and dentition in mammals. But in spite of the modern, more intrinsic, investigations of the morphology of species, there remain cases which baffle the systematist. We know, for instance, species of fleas of which the male is conspicuously different, whereas no distinction whatever from the nearest species has been found in the female. The explanation will turn out to lie deep. We know now that specific differences exist down to the germ-cells. What fifty years ago was a mere suggestion has since been proved to be a fact. It is therefore evident that the investigation of the distinctions between species is far from complete, especially in those classes of animals which it is customary to preserve in a dry state or of which only portions of the body remain available for research, as in the case of mammals, birds, and insects, and that this kind of collection will have to be supplemented by material adequately kept in a liquid, when in future the research departments of museums have at last sufficient room for collections and students. Specific differences are found in soft inner parts, particularly in organs of a glandular nature, of fleas, as well as other insects, and as the diagnoses of species of many invertebrata, for instance worms, are largely based on internals, it is wrong that in other classes the internals are neglected. I dare say it is a question of habit, space, and training. In all, or nearly all, the internal and external distinctions between the species of a family were known, it might be possible to arrive in that family at a morphological species-concept, which would be much more satisfactory for systematic research than having only the physiological concept of the species as an interbreeding community, this concept being inapplicable to dead specimens except evident hybrids.

I have so far considered the species problem only in reference to the multitude of specific populations which are found in the same country, or sympatric species as they are termed by Poulton. But that is less than half the question; in modern times systematists are much more occupied with inquiring into what happens to these populations in other countries. The

robin is met with in other parts of Europe ; it is the same bird, but with a difference. Geographical varieties were already known and recognized as such at the time of the foundation of the Linnean Society ; Drury, in 1773, even applied a trinomial designation to some Lepidoptera : *Nymphalis cardui virginienensis*, *Sphinx ocellatus jamaicensis*. But that the phenomenon of geographical variation has a general application is a comparatively modern discovery, the significance of which is not yet understood by every biologist. The area of distribution of the species is subdivided into minor areas, each inhabited by a subdivision of the specific population—by a subspecies. A. R. Wallace, to whom biology owes so many discoveries, tells us that, when he was down with fever in Ternate, he suddenly saw light in the species question which had puzzled him so long ; the island forms which he had collected from the Malay Peninsula to the Moluccas and Timor during his long stay in the Malay Archipelago stood out before his mind's eyes so well defined that he pronounced them to be the real species. He was right in one way ; they are indeed the lowest category as a population, and if every such geographical population-unit were as sharply defined, as sharply separated morphologically from each other, as those which Wallace described in his treatise on the Indo-Malayan Swallowtail Butterflies, it might be a simplification in systematics to apply the term species to this lowest unit and refer the term genus to the aggregate of such 'species' which clearly represent each other geographically and morphologically. Lowering the categories of classification one step would mean an inconvenient increase of genera. That might be bearable ; but the geographical forms are not all well defined, they do not all remain separate units in the absence of the geographical barrier as do the sympatric species, and if we carried out Wallace's suggestion, a concept of the term species would be substituted which is not the subject of Darwin's 'Origin of Species'. If on the contrary the various geographical forms which have so palpably originated from the same stock are united as subdivisions of a species—there may be special reasons for excluding one or the other—classification is greatly simplified and relationship easy to survey. We have found the introduction of the term subspecies for the geographical race a great convenience. To repeat, within a faunistic area species are in general sympatric populations and subspecies dyspatric populations. The investigation of the distinctions of subspecies from one another has had interesting results, which we found to be alike in such widely different insects as butterflies and fleas : (1) the distinguishing characters of subspecies are of the same kind as those of species, but are less advanced, the difference between specific and subspecific morphological distinctions being one of degree ; (2) subspecies

are not the product of the isolation of mutations ; (3) within the same species we often find a gradation from subpopulations which are not modified to subpopulations which are conspicuously different ; and (4) many instances indicate clearly that the degree of distinctness depends on the duration of the isolation, a subspecies of a geologically old area being more modified than a co-subspecies inhabiting an area isolated at a later period. This gradation suggests that a subspecies is derived from a normal ancestry which was cut off from interbreeding with the parent stock and became gradually modified in its morphology and gradually developed an aversion to interbreeding with other subspecies. The morphological gradation is demonstrated by the subspecies. But have we any evidence that there is also a gradation from complete interbreeding to non-interbreeding in the areas where subspecies come into contact with each other ? Specimens intermediate between subspecies and evidently the product of hybridization are in collections ; but I will here refer only to my own field investigations of this point with subspecies of a mouse-flea which has a continuous distribution in the greater part of Europe and therefore is an eminently suitable subject. To go a-hunting the flea sounds rather funny, but it has its interest and excitement, having even brought me into conflict with the authorities of a certain Swiss Canton where it is strictly forbidden to set traps of any kind. This particular species of flea, *Ctenophthalmus agyrtes* Heller 1896, remains the same from Denmark and Southern Norway to the Lake of Geneva, the Bernese Oberland, and the mountains of Salzburg ; the great contrasts in environment do not seem to have had any influence. In the Dolomites it has become slightly different in the male ; in the Engadine the difference is more distinct ; in the Ticino district another subspecies occurs ; the French Alps are inhabited by a conspicuously different race which descends into the Swiss Rhone valley ; and in Great Britain and Brittany the species is strongly modified. The French Alpine race and the Central European one meet in the Swiss Rhone valley near Aigle, and the specimens from that district suggest that the two races interbreed or that there exists an intermediate race. Which suggestion is correct ? In central Normandy I found the British subspecies to be restricted to the hedges and meadows of the open country, and the Central European species to the wood ; there was no indication of interbreeding. But would they not interbreed if brought together ? This British subspecies occurs southward as far as the Puy de Dôme country and Charente ; the Honble Miriam Rothschild obtained it in numbers at Royat-les-Bains together in the same spot and on the same host with another flea, also in some numbers. This second

flea is unmistakably a derivation of the same stock, but is so different, at least in the male, that I described it as a distinct species. There is no indication of intercrossing whatever. In order to find out what happened to the mouse-flea farther south, I collected in the hills of Tarn, then at low altitude in the Western Pyrenees and at high altitude in the Central Pyrenees, and found everywhere the new *Ct. arvernus* Jord. 1931, but no race of *Ct. agyrtes*. The new species evidently replaces *Ct. agyrtes* in the south-west of France. This is very puzzling, as I have found a subspecies of *Ct. agyrtes* in north-west Spain. If the *Ctenophthalmus arvernus* lived on a widely different host, the case would be explained, for a radical change of host results in strong morphological modifications, as is exemplified by a number of species of fleas. But the hosts of *Ct. arvernus* are the bank-vole and long-tailed fieldmouse as elsewhere, and the specimens of these hosts submitted to a mammalogist are pronounced to be the same as in Northern France. I am doubtful: the hosts the same and the parasites so different! Apart from the fact that *Ct. arvernus* and *Ct. agyrtes* do not interbreed, although the former is the geographical representative of the latter and in earlier ages was a subspecies of it, my investigations have resulted in question marks, as you see. Such and similar points of doubt could be solved by breeding experiments. We have played at Tring with the idea of breeding the British subspecies of *Ct. agyrtes* on mice from the Continent, and the Central European race on British mice, and so on: but circumstances were adverse to carrying the idea into reality. It is distressing not to know the right answer to an important question and only to be able to venture a guess. An experimental station directly in connection with systematics for the purposes of systematics would not be costly to instal and to maintain. The grounds at Tring would be most suitable. But why should I bother about the future when my own future can be but short? The spirit delights to dwell on the time when the dreams will have become realities.

The PRESIDENT: Ladies and gentlemen. I think our visitors at least would like me to follow our usual custom and put to the meeting the usual formula: Is it your pleasure that the thanks of the Society should be given to the various speakers? (Accorded by applause.)

I am sure everyone will agree that we have in this morning's symposium covered a very large and wide field. We have more time available, and hope our foreign guests will give their opinions quite freely on the various aspects of the problem which will be in the minds of many.

Professor H. J. LAM (Leiden) : I am very glad to have the opportunity of saying a few words concerning a field in which I have worked for several years and which I have thought about a great deal recently. We have listened to several interesting speeches with regard to the Concept of Species. It seems to me that the longer one thinks about the subject, and the more one listens to various points of view, the less one knows what a species really amounts to or how it should be considered. That is a little embarrassing, but there is one thing that can be said, namely, that no systematic unit can be considered apart from its history. Of course, one can do taxonomy without considering phylogeny. Every worker in his own particular field has his own way of delimiting systematic units. Histologists will more particularly take the histological pictures of the taxonomists, and morphologists will generally take the morphological findings in order to discriminate species and other systematic units. There must be an endeavour to arrive at the facts in every field, including also Anatomy, Physiology, etc., and to combine as many as possible of the features in every field of study by, say, some statistical method, or some sort of all-embracing description.

I quite agree with Professor Winge that this is all a matter of genetics : that species and other systematic units are based upon genetic features and on genes in general, on combination of genes ; and I do not think there is an essential difference between families, genera, and species. There is only a gradual difference which might be the consequence of their linking and crossing over gradually as a result of the attraction various genes have to each other. As I have said, I see every systematic unit as the consequence of its history, and in a recent paper I used the term 'genorheithrum' as meaning the string of what I call potentialities, a string or flow of, say, genes which cling together and are linked more or less firmly. At any rate, whichever basis one takes or whichever features one chooses for the purpose of discriminating the systematic units, there is one factor which prevails throughout. There is what our Swedish friend Du Rietz would call a discontinuity, and I use that word in an even wider sense than he has done. By discontinuity I mean a gradient similar to that found in floristic boundaries where one has to deal with more or less sudden gradients. This can, I think, also be applied to taxonomy, with phylogeny as the background. Time cannot be eliminated from such schemes of study ; and by the study of a particular cross-section from the point of view of time, one time level at one moment, I think there can be discriminated various sorts of discontinuities. Whatever they may be will, of course, be a subject for future study to which every branch of biology will have to contribute.

This, ladies and gentlemen, is a humble contribution to the splendid addresses to which we have listened this morning. I hope you have been able to follow me. What I have tried to say is that species are not artificial; they are natural; they are in Nature, and there only. In my opinion they can be approached and studied only by tracing the boundaries of the features of every type.

Professor M. J. SIRKS (Groningen) : I should like to comment on Professor Winge's paper. He gave an excellent idea of the genetical and cytological aspect of taxonomy, but it seems to me he has been too sceptical with regard to cytoplasmic matters. The work of Wettstein and others on mosses, tomatoes, the broad bean, and so on have shown that there is something in cytoplasmic genetic differences. I do not think there are genes in the cytoplasm; nevertheless, it seems to me that cytoplasm is of some genetical importance. The study of cytoplasm is much more difficult than the study of genes because analysis is so difficult to make. However, I will not now say more on the point because at the British Association meeting in Nottingham last year I contributed a summary of cytoplasmic inheritance (Botanical Review, iv, 1938, pp. 113-131). I should, in conclusion, like to invite our colleague, Professor Winge, to pay more regard to the cytoplasm from the point of view of genetics and also from the point of view of general taxonomy.

Professor H. BOSCHMA (Leiden) : I was much impressed by Dr. Karl Jordan's account of the differences between the fleas found on species or subspecies of mice. A more or less similar case is that of the Sacculinidae, parasites of crabs. According to Giard each species of crab has its own species of parasite of the group. On the other hand, Geoffrey Smith was convinced that all the parasites of the group on different species of crabs had to be regarded as representatives of one species only. During the course of our studies we came to the conclusion that an intermediate view must be taken: there are many distinct species of Sacculinidae, but a certain species of parasite may infest different species of crabs. Later more material became available and the study of this material points in the direction that the species are far more restricted to the number of their hosts than was known previously. Many of the formerly established species now have to be divided into distinct smaller groups, although the characters of these smaller groups are evident only when sufficient material is examined. This shows again that the further we go with our studies the more difficult they become.

Professor BOHUMIL NĚMEC, F.M.L.S. (Czecho-Slovakia) : It may be of some use if I put forward the point of view of a non-systematist. I have always been under the impression that species grouping was adopted with a view to bringing some order into the immense variability of living things. As done by Darwin that has been a great convenience, especially to the non-systematists, because we could study the species, for instance, in Central Europe, and the study of about 2,000 Phanerogams was not a difficult matter. But later botanists began to draw still further distinctions. There was, for instance, Jordan for *Draba verna*, and about eight years ago there died in Prague a botanist who described many thousand species from Bohemia because he thought it his duty as a systematist to detail everything that could be distinguished from the type. In the National Museum at Prague there are many manuscripts in which the small species Jordanons are described. It is the same with mankind. Linnaeus originally described several species of *Homo sapiens*, but afterwards came to the conclusion that there was only that one species. I think it will be agreed that there now appear to be, even among the white races, several species. One of them is a very high species ; others not so high. When I look round the audience here I realize how difficult it is to say what is a species. I cannot see two really identical individuals among you. And the study of systematic botany and zoology is even more difficult. If we study some species as closely as we can study man, we shall, I think, find that nearly every individual has some individual traits and yet forms a unity. The task of taxonomy is to explain whether these developed as the result of external factors or whether they are genetically formed. That is a study which will take many hundreds of years and provide work for professors of taxonomy younger than those gathered together on this occasion.

Professor W. ROBŮNS (Brussels) : I have listened with much attention to the various contributions to the different aspects of the subject of the Concept of Species. When we compare earlier descriptions of species with the present-day descriptions, we must be struck by the fact that descriptions of the time of Linnaeus, for instance, were brief. They contained only one or two distinctive characters, whereas now when we wish to describe a species, we feel we must include a great number of characters. There are several reasons for this difference. We know, in the first place, many more species than Linnaeus knew. Moreover, there is a certain correlation between the different characters of a species or of a group, so that one or a few main characters may be recognized, which by itself will bring up some other minor characters of secondary value.

That seems to be the result of the use of different criteria. Not only morphological, but also cytological, phylogenetical, and genetical, and even ecological factors are now to be used in the description of species, so that we nowadays have a much better idea of the constellation of characters in a species than Linnaeus had in his time. That is important. We now endeavour to approach the study of species from varying points of view, in order that we may connect them all together and thus obtain a fairly good representation of all the characters.

With reference to the remarks by Professor Winge in connection with the genetical aspect of the problem, I am not a geneticist, but have thought much about the subject, and I realize the importance of genetics in systematics. I think that genes if they do exist—and I am a little doubtful about it—are really confined to varieties. I do not believe they have much to do with the species concept, at least in this respect: that I do not think genes will be found in relation with species characters. That point has been clearly shown by Professor V. Grégoire of Louvain, who in a paper published in 1925 demonstrated that Mendelian segregation is only confined to varietal characters, and has nothing to do with specific characters.

In conclusion, I would like to refer to the work of the late Dr. G. A. Boulenger at the Jardin Botanique de l'État, Brussels, on the genus *Rosa*. You probably know that we in Brussels have the largest herbarium collection of the genus *Rosa* in the world and that this herbarium was brought together by Fr. Crépin, the first Director of the Jardin Botanique de l'État. Dr. Boulenger, who was also, I think, a member of the Linnean Society, worked at Brussels for about seventeen years in the Crépin Herbarium. He used to say that systematics is an art and that the systematist or taxonomist is an artist. He applied that principle to his work. He studied most carefully the numerous specimens of the genus *Rosa*, counting all the variations of the characters of the stems, the leaves, the flowers, etc. After a most critical statistical study of all the specimens, he came to the conclusion that in the genus *Rosa* the species is as real as in any other group, but it is only a question of appreciating the width of variation and individual variability in the specimens. And that is what Boulenger has done both on the herbarium material and on living specimens. I take it he has thus arrived at useful practical results, because it must not be forgotten that systematics has after all a practical aim.

Dr. W. T. CALMAN (late Keeper of Zoology, British Museum) :
If we could imagine an intelligent 'man in the street' straying into this lecture room, what would be his general impression

of this discussion? He would be apt to think that we had all been talking of different things. He would fail to find much common ground in the various speeches that have been made. Now we biologists know that that impression is quite erroneous and that all the speakers have been talking of the same thing. But there is, I think, something to be learned from the fact that they gave an impression of difference of subject. That arises from the circumstance that the meeting point of the various branches of our science—taxonomy, physiology, genetics, palaeontology—is the least worked part of the field, and the part which requires the most study at the present moment.

There has recently been set up in London an Association for the Study of Taxonomy in relation to general biology. I cannot imagine any scientific society which is more needed at present. I only regret that it has not been established under the aegis of this ancient Society of ours, which would be peculiarly suitable for such a study. But I should like to emphasize the fact that in my belief, and in that of many other biologists with whom I am acquainted, the most urgent need is for a systematic exploration of the end-results of taxonomy and the other and more modern branches of science. It is the lack of exploration of that field which has given a fallacious impression of discontinuity to the discussion this morning.

Professor Ø. WINGE (Copenhagen): I should like to say in reply to Professor Sirks that I do not deny that there may be cytoplasmatic differences between species. I know, of course, that botanists sometimes find very great differences, but cytoplasmatic differences between varieties within the species are also well known, so it is not essential to species differences that they are of cytoplasmatic nature. My view is that the principal species differences are gene differences in the chromosomes. There must be gene differences, but there may, of course, furthermore be cytoplasmatic differences.

To Professor Robÿns I would say: It is obvious that not only variety characters do segregate, but also specific characters. The fact that it is easy to observe that variety characters segregate is no proof against the segregation of specific characters.

150th ANNIVERSARY CELEBRATIONS, THIRD DAY.

The Society met in open session at 10 a.m. on 26 May in the lecture theatre of The Royal Institution of Great Britain, 21 Albemarle Street.

Mr. J. RAMSBOTTOM, O.B.E., Dr.Sc., President,
in the Chair

The following papers, prepared for the second symposium, 'Geographical isolation as a factor in Species Formation', were read; followed by a discussion in which the five authors took part (see pp. 292-293):—

'Species Formation and Geographical Isolation.' By Dr. JULIAN S. HUXLEY, F.R.S. (See pp. 253-264.)

'The formation of species among insects in Samoa and other oceanic islands.' By Prof. P. A. BUXTON. (See pp. 264-267.)

'The concept of species and geographical isolation in the case of North Atlantic Patellas.' By Dr. E. FISCHER-PIETTE. (See pp. 268-275.)

'Some problems of geographical variation and species formation.' By Dr. BERNHARD RENSCH. (See pp. 275-285.)

'Geographical isolation as a factor in species formation, and its relation to certain insular floras.' By Dr. C. SKOTTSBERG. (See pp. 286-292.)

SPECIES FORMATION AND GEOGRAPHICAL ISOLATION.

By Dr. JULIAN S. HUXLEY, F.R.S., F.L.S.

Most species are true biological units, marked off by the fact of their not interbreeding with others. They are discontinuous entities. Yet we are compelled to believe that they have arisen directly from other species. Life is indeed under one aspect a continuum. Every individual and every species is a continuation of another. Species that arise by hybridization have two parents, as do individuals that originate sexually: but the continuity exists equally, whether the parents number one or two.

Yet discontinuity is a more obvious fact of life than is continuity. The discontinuities of individuals and of species force themselves on the untrained attention, and that of cells makes a third basic discontinuity, discovered by research.

None of these discontinuities, however, is absolute. Every biologist knows the limitations of the cell-theory and the borderline cases between independent individual and subordinate part; and the progress of taxonomic research has brought to light numerous cases, of several different kinds, of the incomplete discontinuity of species. These exceptions are, of course, what we could expect in a world of reproductive continuity and evolutionary transformation.

Looked at in the broadest possible way the species problem thus becomes the problem of the establishment of group discontinuities in the evolutionary continuum. This means that it is not enough to study the groups which we call species: it becomes of equal importance to study the gaps between the groups.

In the origin of such biological discontinuities some form of isolation appears to be necessary. The three main types of isolation are genetical, ecological and geographical. Sometimes the isolation and the discontinuity are one and the same, and are complete from the outset. This is so in certain cases of genetic isolation, as when a new species arises by allopolyploidy or by a single mutation causing intersterility with the parent form. In other cases of genetic isolation, such as inversion and translocation, the barrier is not complete, but must be gradually widened later if specific discontinuity is to arise.

Ecological isolation has been chiefly studied in relation to physiological races of fungi and insects adapted to different hosts or different food-plants. It is probable that it will be found operative also, in some groups at least, in relation to other environmental differences. It clearly involves some degree of spatial isolation, and may grade into the geographical process.

Geographical isolation has been the most thoroughly investigated. It involves groups which inhabit distinct regions, not merely distinct habitats within a region. These distinct regions, however, will almost invariably differ somewhat in climate, soil, vegetation or other factors, so that, in general, ecological isolation will also be operative. However, the spatial isolation is here the primary and major factor, while the ecological is, originally at least, subsidiary.

The practice of taxonomy has been radically modified through a careful study of the geographical factor. Broadly speaking, the first phase of modern taxonomy, from the Renaissance through Ray and Linnaeus until after the middle of last century, was characterized by a concentration on differences. In professional jargon, it was a phase of splitting. As new forms came to hand they were given new specific names whenever they could be reasonably distinguished from their nearest relatives.

As collections became more complete, however, doubts began to arise. Many forms which had originally seemed distinct enough were found to be connected by intermediates : and the number of forms which could at a pinch be distinguished began to grow unconscionably large. Gradually a new doctrine arose—that of geographical replacement. When a group of closely allied forms was investigated, and the separate forms were found not to overlap but to replace each other in different portions of a larger region, the whole group came to be treated as the species, the single forms as geographical subspecies into which the group had differentiated. Of late years forms which may be called physiological, ecological or genetical subspecies have also been distinguished, so that we may say that the concept of the compound or polytypic species, partially differentiated into subspecies, has been in principle generalized. By this means the total number of species recognized has been very materially reduced. Rensch wishes to confine the term 'subspecies' to the geographical category, but there seems no valid reason for excluding forms which have originated by other methods of isolation. We may anticipate that the principle will be still further extended by the establishment in palaeontology of chronological subspecies, differentiated in time.

With geographical differentiation, Rensch has drawn attention to an extension of the principle to groups consisting of forms differentiated to the stage of obvious species, but equally obviously showing geographical replacement.

Various terminologies have been proposed, but I would suggest the following as the most general and involving the least break with accepted terminology. I here confine it to geographical forms, though it can be extended to other types of differentiation :

<i>Subspecies :</i>	Forms showing geographical replacement, but either connected by intergradation or, if isolated, not differentiated sufficiently to merit specific rank.
<i>Monotypic Species</i> (Rensch's <i>Ar</i>) :	Not differentiated into subspecies.
<i>Dipolytypic Species</i> (Rensch's <i>Formenkreis</i>) :	Differentiated into two or more subspecies.
<i>Supra-species :</i>	Groups of forms showing geographical replacement, but with some forms showing differentiation certainly or probably meriting specific rank. (Intermediate between polytypic species and geographical subgenera.)
<i>Geographical Subgenus</i> (or <i>Genus</i>) (Rensch's <i>Arten-</i> <i>kreis</i>) :	Groups of related forms clearly meriting specific rank, but showing geographical replacement to a degree which makes it certain they have arisen by geographical differentiation.

Rensch rightly points out that the geographical genus is the highest taxonomic category with a real existence, further categories from genera (in the accepted usage) upwards being artificial concepts. He also draws attention to the need of retaining purely neutral terms, such as *form*, *group* and *population*, to denote units of any size or nature, in addition to more carefully defined and technical terms such as *subspecies*, *species* or *genus*.

In spite of Goldschmidt's objections (which Rensch has shown to rest upon misapprehension) it seems clear that geographical differentiation is one of the normal methods of speciation and probably the commonest (in animals at least), and that accordingly geographical subspecies may be (though by no means all of them will be) 'species in the making'. A further corollary is that all degrees of geographical differentiation between groups may be expected, from such slight differences that not the most inveterate splitter would wish to give them a subspecific name up to full species and beyond.

Most of the consequences of the differentiation due to geographical isolation are well known. In general, the completer the geographical barriers the greater and sharper is the differentiation that results, whereas the existence of intergrading zones allows a freer flow of genes from one form to the other. This is well shown in one of Sumner's *Peromyscus* cases, where an island subspecies whose colour is adaptively related to the white sand of the background is much paler than the mainland form on beaches of the same colour, because this latter intergrades with a dark inland form.

It has been suggested that isolation *per se* favours differentiation, but the evidence on the whole points to most minor taxonomic differentiation being determined by selection, and so related either directly or indirectly (consequentially, by what Darwin called correlated variation) to slightly different environmental conditions.

The chief exceptions appear to be the following:—First, where considerable variation exists in a parent population, and a new area is colonized across a relatively complete barrier, a limited sample, not fully representative of the original form, may give rise to the new subspecies. Perhaps the best-known examples of this come from the snails of the genus *Partula* from Tahiti, but many striking cases are known from mammals, birds and Lepidoptera, where a form that is usually diphasic is represented in certain areas by one phase only. Secondly, as Sewall Wright has shown, in numerically small and well isolated groups mutations may be perpetuated that we may call accidental, in the sense that they are not selectively related to the environment. This is in correlation with the

empirical fact that on small isolated areas (e.g. islands) subspeciation proceeds more rapidly than on larger ones.

Thus isolation may favour chance divergence either at the time of origin of a new form or subsequently. Rensch and others have also shown by careful studies how the end members of chains of forms that are completely connected by gradations may, if brought together, either artificially or by natural migration behave as completely differentiated species, and fail to interbreed. Examples are known from birds, butterflies, beetles, etc.

There are, however, one or two points which do not seem to have received the theoretical attention they deserve. In the first place there appears to be a real biological difference, and one which we should expect on *a priori* grounds, between closely related forms which have differentiated geographically and have remained isolated in different regions, and those which now overlap geographically, occupying different ecological niches in the same region, whether they have originated by ecological or physiological differentiation in the same region or have migrated into it subsequently to their original differentiation.

In the most general terms we should expect the geographically overlapping forms to show the stronger barriers to intercrossing. These barriers may be genetic (inter-sterility), or reproductive (different breeding times or, in plants, adaptations to pollination by different insects), or behaviouristic (in higher animals, as by different mating instincts, recognitional patterns, songs etc.). Some of the most striking concern birds. Geographically overlapping species of birds that are closely related, when of similar appearance often possess markedly different songs, and in many other cases show markedly different recognitional patterns. Geographically differentiated species of birds, however, may, in spite of marked general differentiation, show no barriers to fertile interbreeding on being brought together by migration. The crows of Europe and the flickers of America demonstrate this latter state of affairs.

The evolutionary reason seems clear. If the overlapping species are in point of fact adapted to different ecological requirements it will be a biological disadvantage for them to cross. Their offspring, even if fertile, would *ex hypothesi* be less well adapted than either of the parent forms. Geographically isolated forms, however, do not normally have the chance of interbreeding, so that the same selective situation will not arise. Further, their degree of adaptive ecological differentiation is not likely to be so great, so that, if brought together later, selection will not operate so strongly against their hybrid progeny. There will, of course, be numerous

exceptions to this rule, notably through geographically isolated forms developing characteristics which prevent them from interbreeding (e.g. the two species of tree-creeper (*Certhia*) in central Europe), but the general tendency remains.

Cases such as that of the crows and flickers lead on to a second point. In both of these, two well-differentiated forms have been brought together as a result of post-glacial changes of climate. The observed result is that the two forms remain well-marked and constant over most of their areas, but are separated by a relatively narrow zone of interbreeding where every possible type of Mendelian recombination between the two 'pure' forms is to be found. What would seem remarkable is the narrowness of this zone. With the crows it is often less than 100 miles wide, although its length is several thousand miles.

The question thus presents itself as to how the narrow zone is maintained and how the genes of either form are prevented from spreading freely into the area of the other. It is possible that the answer is to be found in the limited time that has elapsed since the two forms came into contact, but the narrowness of the zone makes this somewhat dubious when we remember that interbreeding must have been going on for several (five to ten) thousand years.

The same problem, but in a more acute form, is raised by the existence of intergrading zones between adjacent subspecies that are not actually isolated by geographical barriers. These are well marked in many species of higher animals which inhabit large continental areas. The shrikes (*Lanius*) and deer mice (*Peromyscus*) of North America, or the wrens (*Troglodytes*) of South America, provide well-analyzed examples. But though these zones of intergradation have been frequently described, little attention has been paid to their biological meaning. Yet they present obvious difficulties. We are confronted with two distinct and relatively uniform populations inhabiting comparatively large areas, which are separated by quite narrow zones where interbreeding and consequent intermediate forms occur. In an example in *Peromyscus* investigated by Sumner the intergrading zone is only three miles wide. That it is actually a zone where two differentiated types interbreed is further shown by the fact, which does not seem to have attracted sufficient attention, that the variability of its population is markedly higher than that of any sample of the two differentiated subspecies on either side of it.

A possible answer is that the two forms have not always been in contact, but have developed in isolation, the contact having been achieved later by migration. However, the frequency of such cases, even in continental areas where no sharp geographical or ecological barriers exist, and which

must have been habitable for long periods, argues against this easy view.

If we assume that the groups have been in contact since their divergence the question at once arises, why and how these narrow zones are maintained? The environmental conditions change gradually, yet the biological population changes abruptly. As interbreeding is going on, genes must be flowing across the zone in both directions, a conclusion supported by what we have previously said as to the greater effect of selection on populations that are fully isolated and show no interbreeding zones. Yet the narrowness of the zones indicates that there is some barrier to the freedom of the genetic flow. What is the biological basis of these barriers and what is the biological reason for their existence?

So far as I am aware only one plausible explanation has so far been advanced. Timoféeff-Ressovsky, in his genetic analysis of geographical variation in certain beetles, showed that some gene-combinations were more viable and more successful than others, and that on the whole it was these combinations which were realized in the existing geographical subspecies. If this observation can be generalized it provides a formal explanation of the facts. Selection in two ecologically distinct regions favours two gene-constellations, but acts against intermediate combinations. Superior viability will thus extend the area occupied by each favoured form beyond the region to which it is primarily adapted, so that two relatively uniform types will occupy most of the area, and the intermediate forms, though constantly generated by intercrossing, will be restricted to the narrowest possible belt.

Another explanation may be suggested, which may operate in addition to that just mentioned. If two differentiated but interfertile populations meet as a result of migration, and one (A) has a slight selective advantage over the other (B), then A might slowly increase its area, while the intergrading zone is pushed into B's area without increasing appreciably in width. I believe that the theoretical analysis of such a situation would prove fruitful, while in certain cases observational evidence as to such a shift of the intergrading zone could be obtained.

The general problem, however, can only be clearly envisaged in relation to a further series of facts. Following on the pioneer work of various nineteenth century animal taxonomists, it has now been firmly established that a regular geographical variation is shown internally by many groups.

In most cases so far investigated this internal variation has not been traced further than to the mean values of various characters of the constituent sub-groups. Rensch has recently collected a large body of data on this aspect of the problem.

He has shown that within groups of subspecies or species showing geographical replacement geographical regularities affecting colour, size, proportion of extremities etc. in certain groups, some of which have been long known under such names as Bergmann's, Allen's and Gloger's rules, do hold in the considerable majority of cases.

In a few cases, however, the analysis has been pushed still further—e.g., by Sumner in deer mice, Alpatov in bees, or Christy in buffaloes. Their work has shown that a continuous slight change of character may occur within single groups (subspecies or apparently monotypic species). In *Drosophila*, genetic analysis has shown that wild populations which are geographically homogeneous from the standpoint of ordinary taxonomic practice may in point of fact differ from place to place in adaptive characters such as temperature-resistance related to local climate. In forms with sharply marked 'phases' (arctic fox, guillemot) it appears that the proportion of the two types may vary geographically in a regular way.

In one case, namely *Peromyscus*, the two methods of analysis have been combined. It is found that the means of subspecific characters may show geographical regularity, and that in addition a less obvious trend in the same direction may manifest itself within the separate subspecies. In such a case the graphic representation of the geographical variation of a character will resemble not a staircase but a stepped ramp, the subspecies showing a gentle slope, the zones of intergradation a steep one.

For such geographical regularities of variation I propose the term *cline*. Clines may then be either *inter-group* (or *group*) when they concern the mean values of group characters, or *intra-group* (or *internal*) when the group itself is not geographically uniform in genetic composition, but shows regular gradation.

Since the above was written, my attention has been drawn to the interesting work of Reinig ('Elimination und Selektion', Jena, 1938). In this, while adducing numerous valuable examples of clines (which he calls *merkmalsprogressionen*), he denies that they have any adaptive correlation with climatic gradients. For him, they come about as the result of the expansive migrations produced by pleistocene climatic changes. During such migrations, he claims, a progressive depauperization of the variance of the species occurs, resulting in clines (e.g. in decrease of size) from the centre of distribution to the periphery reached by migration.

While in some cases this type of cline does seem to occur, I feel that adaptive climatic and ecological clines also exist.

I foresee that in its next phase detailed taxonomy will concern itself intensively with the investigation of clines. In so doing it will be continuing the phase of synthesis initiated by the relegation of forms showing geographical replacement

to the rank of subspecies and their union into comprehensive species. But it will give a better picture of the resultant polytypic species. As matters stand at present the separation and accurate description of subspecies is usually regarded as a sufficient end; but if they can be related by the establishment of inter-group clines between them we shall obtain a unified picture, pregnant with biological meaning, of the polytypic species to which they belong—a picture which in most cases is now conspicuously absent. In many exhaustive modern taxonomic studies (e.g. Hartert's Palearctic Birds) the species is not even described as such, and we are given a catalogue of the various subspecies, with little or no attempt at a synthesis based on their interrelations.

As an example of the illumination which may be expected to result, I will quote the example of the cole-tits (*Parus ater*). The three subspecies of western Europe, Continental, British and Irish, are characterized by numerous differences in colour, which are minutely described in current text-books. Analysis of these descriptions shows that the essential difference consists in a progressive increase, as we pass westward, in the amount of yellow (lipochrome) pigment in the feathers of the adult. Further analysis shows that this depends on varying rates of decrease in the amount of the yellow pigment during ontogeny, the rate being least rapid to the west. Precisely similar considerations apply to the African buffaloes described by Christy, the ontogenetic process here affected being the change from red to black, which begins earlier and goes to a further extreme in dry conditions, and is almost entirely inhibited in moist forest environments. If, as appears probable, intra-subspecific clines also occur in such cases, geographical differentiation is illuminated as a process of beautiful regularity related on the one hand to the environment and on the other to the mechanism of individual development.

Once we have mapped the clines within a series of related polytypic species or species-groups, we shall at last be in a position to envisage the problem of evolutionary differentiation in its true relation. I pointed out at the outset that life must be regarded as a continuum broken by discontinuities of varying extent. It is only within natural units, the geographical genera and lower categories, that we can study both the continuities and the discontinuities, the regular changes and the gaps, at one and the same time. The partial discontinuities of intergrading zones, the geographically complete but biologically incomplete discontinuities between fully isolated subspecies, and the biologically complete discontinuities between related species with geographical replacement, will all take on new meaning when studied in relation to the regularities of inter- and intra-group clines.

Comparison of related forms, based on standardized biogeographical mapping, will also enable us to say whether the 'joints' between subspecies tend to recur at the same spots on the map, or whether initial accident or later migration obscure any such regularity.

The study of clines will also provide us with a subsidiary method of taxonomic description which will obviate certain present difficulties. For one thing, it will make it unnecessary to erect so many subspecific forms, and will make clear the proper relationship of other local forms which, though distinct, differ so slightly from their neighbours that they cannot possibly be given a separate name (e.g. the wrens inhabiting Fair Isle, which are intermediate between the Shetland subspecies and that of the Orkneys and the mainland). The formidable alternative would seem to be the establishment of quadrinomialism, with 'subspecies' as final term.

Then specification by clines in addition to that by geographical groups will correct the psychological tendency to attribute undue importance, distinctness and uniformity to a form which has received a Latin name. Further, in cases of purely ecological variation it will make it unnecessary to give subspecific names, which not only burden the nomenclatorial literature but confuse the issue of geographical as against ecological differentiation. The different forms can be given the title of varieties (ecological varieties, ecotypes, etc.), but these would not be included in the standard trinomial nomenclature, and the important taxonomic specification could be made by means of ecological clines.

This type of differentiation would probably apply to various land-snails among animals, while in plants it appears to be widespread and possibly of more biological importance than geographical differentiation. The recent careful analysis by Gregor of the variation of *Plantago maritima* provides a good example.

Finally, while specification by named subspecies gives a description of groups and their complex of characters, specification by clines will permit the description of the variation of single characters, which, as analysis has already shown (e.g. in various birds), may vary independently of each other in different geographical directions.

One other more general point may be made before concluding. While isolation permits and in general promotes differentiation, the degree of differentiation achieved depends mainly on selective factors; and these will frequently be of a biological nature as opposed to factors of a physical (climatic) order. Various studies, for instance, have shown that reduction in the intensity of pressure by predators permits a greater degree of evolutionary radiation (Cichlid fish in certain African

lakes ; many groups on oceanic islands, e.g. among insects in Polynesia, or birds such as the Geospizids on the Galapagos ; marsupials in Australia). The intensity of predator pressure will also directly affect the development of such differentiations as cryptic resemblance to background.

The degree of isolation is itself also determined by biological as well as purely geographical factors : for instance, Rensch has shown that in birds the amount of subspeciation is greatest in small and non-migratory forms, least in large and wide-ranging forms.

Summing up, we may reach the following general conclusions, some of which are inductions based on known facts, others deductions which we may expect to see verified by further study:—

(1) Within any interbreeding group inhabiting a geographically diversified area we may expect to find some diversification of character brought about by selection in relation to climatic and other environmental differences. This diversification may concern invisible (physiological) characters, e.g. temperature resistance ; or visible characters directly related to environment, e.g. cryptic resemblance ; or visible characters correlated with invisible physiological adaptations, e.g. the darker colour of warm-blooded animals in humid regions. In the simplest cases this geographical variation will be continuous, to be described in terms of clines

(2) Any geographical isolation will tend to insert some degree of discontinuity into this continuous variation. It is probable that mere distance will, with relatively non-mobile forms, produce partial discontinuities, resulting in distinct subspecies (which may still show internal variation in the shape of gradual, geographical clines) separated by sharp transitional zones (steep genetic clines).

(3) In addition to broad geographical clines continuous ecological clines may be developed, notably in plants and some lower animals.

(4) Complete or virtually complete isolation will often result in the production of distinct geographical forms without zones of intergradation. These may be of any degree of distinctness, from forms too trivial to merit subspecific names up to full species.

(5) The distinct geographical units thus differentiated will be interrelated by inter-group clines, related to the mean values of the group characters. In general, this inter-group geographical variation will run in the same direction as the intra-group clines, but will show a steeper slope.

(6) Geographical isolation may also promote non-adaptive differentiation. This may be (i) initial, due to colonization

by a non-random sample, or (ii) subsequent, due to the preservation of non-adaptive mutations in numerically small isolated groups.

(7) Subsequent to differentiation initiated by isolation, migration (and human interference) frequently alters the ranges of isolated groups, and may frequently cause the meeting or overlap of originally separated forms, with or without resultant hybridization. Expansive migration, according to Reinig, may also lead to progressive loss of genes due to the migrants constituting a non-random sample, and this will produce a series of clines radiating out from the centre of distribution to the periphery.

(8) When ecologically distinct and closely related species overlap geographically, whether from the outset or as a result of migration subsequent to differentiation, selection will increase the biological discontinuity by strengthening the barriers against interbreeding.

(9) Biological as well as geographical factors help to determine the degree of isolation, e.g. degree of mobility.

(10) Biological factors help to determine the degree of differentiation initiated by isolation, e.g. low intensity of selection-pressure from predators permits greater evolutionary radiation.

(11) The chief effect of geographical isolation thus seems to be the insertion of biological discontinuities of different degrees of completeness into populations showing continuously-varying adaptive differentiations, thus accentuating the closeness of adaptation; and the increasing of diversity by adding some degree of non-adaptive differentiation.

THE FORMATION OF SPECIES AMONG INSECTS IN SAMOA AND OTHER OCEANIC ISLANDS.

By Professor P. A. BUXTON, London School of Hygiene
and Tropical Medicine.

THE characteristics of the fauna of an oceanic island have been known since 1880, the date of the first edition of Wallace's 'Island Life'. Perkins's introduction to 'Fauna Hawaiensis' is our best authority on the insects of an oceanic island. More recent work has added little to them, except that we do not now regard oceanic and continental islands as holding sharply defined 'species', but rather as the extremes in a series of grades. An oceanic island may be defined as one which is not a fragment of an ancient land mass, which is surrounded

by deep water: the terrestrial fauna and flora reached it by crossing the ocean.

Among the conditions of life which prevail there are at least two which tend to influence the production of species.

1. *Isolation*. There is a 'major isolation', due to remoteness from other land, and in particular from continents with large complex faunas. Moreover, the creatures in one gulley, or in the crowns of one group of palms or *Pandanus*, perhaps never mix with those in a similar spot a few hundred yards away. The equable climate of oceanic islands, and the fact that (till the last century) human interference was generally slight, tends to reinforce the 'minor isolation', which perhaps occurs in all parts of the world, but very noticeably in tropical islands.

2. *Paucity*. It is a general truth that the total number of insects, and, indeed, of all forms of life, in an oceanic fauna is low. The Hawaiian Islands are known to have 4620 species (Bryan), Samoa 1603 (Buxton), the Seychelles, not totally oceanic, 2090 (Scott). It is difficult to find comparable figures for a small area in a tropical continent, but one may assume that the total number of insects would be several times greater. The paucity extends to major taxonomic units, families, tribes, etc.

In particular it is noted that many groups of predatory animals are not found in oceanic islands, and it is clear that, at least in this respect, the competition between species and the struggle for existence is less in these islands than it would be on a continent. In general the terrestrial mammals (many of which are insectivorous) and the amphibia are absent from oceanic islands, or at least very poorly represented; many other predatory groups of birds or insects may also be lacking. From the Samoan fauna one notes the absence of Accipitrine birds, of wood-swallows (*Artamus*) and true swallows (*Hirundo*), all of which occur in Fiji. There are no native terrestrial mammals, no Amphibia, and only one snake. Among insects many predatory families are absent, e.g. Mantidae and Cicindelidae (tiger-beetles). But in spite of these absences Samoa has a considerable number of insect-eaters, such as fly-catchers, white-eyes (*Zosterops*), a swift (*Collocalia*), an insectivorous bat (*Emballonura*), ten sorts of lizard (Geckonidae and Scincidae), and many Odonata (dragonflies) and spiders.

The effect of these conditions upon the production of species has apparently been as follows:—

1. *The proportion of endemic forms* in an oceanic fauna or flora is very high. The following proportions of insects are endemic: in Hawaii 82 per cent., in Seychelles 65 per cent., in Samoa 49 per cent. Similar figures could be quoted for

particular groups of insects in St. Helena, Fiji, the Marquesas, etc.

2. *Remarkable and peculiar types* have arisen in some oceanic islands—for instance, endemic genera (and occasionally higher taxonomic units) which cannot be satisfactorily placed in systematic relation to forms known from the rest of the world.

3. *Certain species of insects are extremely variable.* In dealing with Samoan geometrid moths Prout called attention to the great variation, and numerous directions in which it developed, in *Cleora samoana*: even among moths taken at one place and on one night the range of variation was remarkable.

It frequently happens that the insular members of a genus are not only variable but also numerous, many of them being confined to particular parts of an archipelago. One then has a 'complex' of forms in which it is extremely difficult to delimit species. In the Seychelles and Samoa such complexes occur, but they are neither numerous nor elaborate. Examples are known among Lycid and Eumolpine beetles in Samoa. Hawaiiia provides a great contrast to Samoa and the Seychelles, for its insect fauna contains many of these complexes, in some of which the species are very numerous. The genus *Prote-rhinus* (Coleoptera related to weevils) was known to contain 130 endemic species when Perkins wrote. Many were variable, the variation being in part geographical (in those species which occurred on several islands), and related also to food-plant; but it was frequently observed that there was much variation in a series from one place to one plant, and it was a matter of great difficulty to arrive at specific determinations. There is little or no tendency for a group which has produced many endemic forms (and even complexes) in one archipelago to do so in another. Note the contrast which the Carabidae (ground-beetles) present in this respect:—

Archipelago.	Genera.		Species.		Total.
	Not endemic.	endemic.	Not endemic.	endemic.	
Hawaiiia (Perkins) ..	5	34	6	204	210
Seychelles (Scott, 1933).....	6	2	7	2	9
Samoa (Buxton) ...	10	0	9	6	15

It is not difficult to suggest an explanation which appears to cover most of these facts. Rather few ancestral species reached the oceanic island, crossing the sea by accidental means: this process is still continuing. There must be much selection among species which succeed in landing, those which breed in rotten wood, humus, etc., tending to survive; specialists (parasites, gall-makers etc.) to die out. The species which

established themselves long ago had opportunities of evolving, and filled many unoccupied niches. The numerous endemic species which have originated on the island, and the existence of complex groups of variable species, are generally regarded as evidence of the freedom under which the insects have evolved and of the relatively slight struggle for existence. This view is probably true in the main, but should be accepted with some reserve. Everyone would admit that the comparative absence of predatory forms must make life easier for many insects; but it is not by any means clear that an insect which is dependent on a particular food-plant meets less competition in an oceanic island than on a continent. There has been a tendency to over-emphasize the absence of competition in oceanic islands. It is only when more information about life-histories and ecology is available that it may become possible to assess the competition.

It is important to remember that many of the endemic species are not unusually variable, and that many of them have evolved, without giving origin to a large number of forms, into creatures so different from other known forms of life that they have to be referred to monotypic endemic genera. For instance, among the Samoan Micro-Lepidoptera Meyrick found 137 species; 90 of them were endemic, and distributed among 54 genera, 8 of which are monotypic.

A very short list of relevant papers is appended:—

- BRYAN, E. H. 1934. The contributions of Bishop Museum to Poly-
nesian biogeography. Contribution à l'étude du peuplement
zoologique et botanique des îles du Pacifique. *Soc. Biogeogr.*
Paris. Vol. iv.
- BUXTON, P. A. 1935. Summary, Insects of Samoa, part 9, fasc. 2.
British Museum, London.
- HESSE, R. 1937. Ecological animal geography (authorized rewritten
translation by W. C. Allee & K. P. Schmidt). New York.
- MEYRICK, E. 1927. Insects of Samoa, part 3, fasc. 2. British Museum,
London.
- MUMFORD, E. P., & ADAMSON, A. M. 1934. Entomological researches
in the Marquesas Islands. Contribution à l'étude du peuplement
zoologique et botanique des îles du Pacifique. *Soc.*
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- PERKINS, R. C. L. 1913. Introduction, being a review of the land
fauna of Hawaiiia. Vol. i, *Fauna Hawaiiensis*, Cambridge.
- PROUT, L. B. 1928. Insects of Samoa, part 3, fasc. 3. British Museum,
London.
- SCOTT, H. 1931. Summary and general conclusions regarding the
insect fauna of the Seychelles and adjacent islands. *Proc. Linn.*
Soc. Lond. 1931-32, pp. 136-140.
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of the Seychelles and adjacent islands. *Trans. Linn. Soc.*
Lond. ix, pt. 3, pp. 307-91.
- WALLACE, A. R. 1880. Island Life.
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THE CONCEPT OF SPECIES AND GEOGRAPHICAL ISOLATION IN THE CASE OF NORTH ATLANTIC PATELLAS.

By Dr. E. FISCHER-PIETTE, Paris.

THE limpets of the genus *Patella* have always been well known as a difficult subject for systematists, and there are striking disagreements between the authors. I have tried to get to the bottom of this question by looking for new morphological characteristics (concerning chiefly the radula ribbon) and above all by studying in the field very large populations on long stretches of the coast-lines of England, France, Spain, and North Africa. I have already partially published the results (1935). To-day I will add some new observations, particularly from Corsica, as well as some general remarks after utilizing some documents relative to the Macaronesian archipelagos.

One of the results obtained is to show that the question of systematics and the geographical question are closely linked together. At first sight the profound disagreements that separate scientists would almost seem to be a question of two divergent and well-known mentalities, that of the splitters and that of the lumpers. But in reality it is a question of locality. You are of necessity a splitter in some districts, as was Dautzenberg in Brittany, whereas you are of necessity a lumper in other districts, as was Dr. Paul Fischer on the Biscayan coast. Let us see why it could not be otherwise.

Momentarily we will leave on one side the Macaronesian archipelagos and the possible part played by geographical isolation, and consider only the European-African continental coasts (including the adjacent islands: the British Isles, Corsica, etc.). Their study will help us to understand later the possible part played by geographical isolation.

First, let us be 'splitters'. For that I must take you to certain regions, and we must avoid others. For example, let us go to Cornwall in England, to Brittany in France, to northern Corsica, to the Habibas islands opposite Oran, etc. Studying the *Patellas* there, we are obliged to recognize a total of seven quite distinct species: *P. vulgata* Linn., *P. intermedia* Jeffreys*, *P. aspera* Lam. (= *P. athletica* Bean)*, *P. caerulea* Linn., *P. ferruginea* Gmelin, *P. safiana* Lam., *P. lusitanica* Gmelin.

* J. R. le B. Tomlin has established (1923) that *P. intermedia* Jeffreys 1865 is *P. depressa* Pennant 1777. I use here the name *intermedia* to avoid confusion, as the name *depressa* has been used by many authors (such as Jeffreys, Dautzenberg, and I in my previous papers) for the form named *P. aspera* by Lamarck in 1819 and *P. athletica* by Bean in 1844.

There are numerous characteristics by which they differ from one another—in their shells, in their anatomy (the study of the radula gives very definite results) (Fischer-Piette 1935), and also in their ecology.

For example, one word now on the ecology of the three species occurring in the Channel, *P. vulgata*, *P. intermedia*, and *P. aspera* (= *P. athletica*).

Concerning the horizontal distribution, *P. vulgata* is found further East into the Channel, and penetrates deeper down the estuaries, than *P. intermedia* and *P. aspera* (= *P. athletica*). Concerning the vertical distribution, the three species have the same low limit (low water of spring tides), but different high limits: *P. aspera* (= *P. athletica*), high limit, low water of neap tides; *P. intermedia*: high water of neap tides; *P. vulgata*, high limit surpassing by one metre that of *P. intermedia*.

I want to point out that, although each of the three species has its own distribution, they have in common one notable part of their areas at the low levels of exposed coasts. There they are found closely mixed together on large territories. This does not prevent them from remaining there perfectly distinct one from the other. There are no specimens of hybrid aspect found there.

Now let us be 'lumpers'. We shall leave the districts where we were, to go to others, such as the Isle of Wight (namely Freshwater Bay), the French and Spanish Biscayan coast, the coasts of Roussillon (French Catalonia), the region of Bonifacio in Corsica, etc.

There we may notice this fact that it is no longer possible to recognize the separation between the various species quoted*. All the intermediates are found between them, considering the conchological characteristics as well as the anatomical ones. Even the differences in the limits of distribution disappear.

There is another thing. In these districts there are not only representatives of the various species mentioned above, and intermediates between them, but there is also an accentuated variation in new directions, so that we find unaccustomed types of shells, of radulas, etc.

For example, I found at the Isle of Wight particular *Patellas* that I had not seen either in Brittany or in Devon and Cornwall,

* That does not concern *P. safiana* Lam., which does not live in these places. The intermediates between *P. ferruginea* and the other species, of which I did not speak in my paper of 1935, have been since then observed at Bonifacio. There are also at the Azores intermediates between *P. lusitanica* and *P. aspera* Lam. on one hand (var. *d.* of *P. aspera* Lam., Simroth), and between *P. lusitanica* and *P. ferruginea* on the other (*P. nidulina* Loc., of which the specimens are in the Muséum National d'Histoire naturelle).

but which have somewhat a resemblance to certain forms of *P. caerulea* of the Mediterranean.

A striking diversity may be specially observed on the Biscayan coast between one locality and another in the appearance of the limpet-populations. I have visited different localities of France and Spain, and I found that there is a special dominant-type in each locality. Now an intermediate between two well-known species, then a divergent type. There is a very curious fact at St. Jean de Luz. This locality possesses as a particular type, *Patellas* which are more or less similar to *P. caerulea* and some of which are the same as this Mediterranean species and its varieties. Farther on the Spanish coast I found no more *P. caerulea*, and it seems that we must go to the Straits of Gibraltar to find it again (Hidalgo, Nobre).

Then, being in those regions, if we now try to circumscribe the species, we are brought to consider as only one species the whole of *P. vulgata*, *intermedia*, *aspera* (= *athletica*), *caerulea*, *ferruginea*, and *lusitanica*. That grouping is supra-Linnaean and would enable one easily to take as a taxonomical unit the section *Patella* sensu stricto of Pilsbry*.

Then at the moment we no longer know what to do with the word *species*. Let us get rid of it for some minutes, so that we may express a first conclusion. Let us consider the 'entity' *P. vulgata*, the 'entity' *P. intermedia*, etc. The statement is this :—

In some districts there are no separations between these entities; there is intergrading. In other districts there are clear-cut separations in spite of overlapping habitats.

We see that these cases are even more difficult than those which Einar Du Rietz (1930, p. 371) presents as being 'the most difficult cases that may confront a taxonomist', viz. the cases where the species occupy 'different distribution-areas or at least different habitats in the same distribution-area', but where those areas have a common portion where the species flow 'together into one vast syngameon'.

We are confronted here with species whose general repartitions are distinct, but overlap, but the syngameon exists only in certain regions of their common territory: in the remaining common territory the species keep perfectly distinct.

In the case cited by Du Rietz, one may accept his suggestion to define a 'heterofacial species' with 'different subspecies', but here we cannot treat those entities as geographical subspecies since they are able to keep distinct in a common geographical area. Maybe that they must be considered as mutations? That would not solve the question of knowing

* After studying the collections of the Paris and Madrid Museums, and Mr. Pallary's collection, I am inclined to think that some more species must be aggregated to the above-mentioned complex.

why those entities would form a syngameon in some districts and not in others.

My tendency is to consider these *Patellas* as belonging to one large *species* (espèce-souche) able to split into several smaller *species*; the splitting has been accomplished in certain districts and not in others. (The cause of these differences is to be investigated: I think it is a question of lithology.) The variability, which is very strong in the districts where the separation between species has not taken place, is extremely sensitive to the local conditions: those conditions make it work in very diverse directions, resulting in particular forms. Between the peculiar types thus obtained, some have perhaps only the potentiality of varieties or the value of occasional hybrids, while some others are potential species. The latter possibility clearly appears in the case of *Patella caerulea*, as, at the Isle of Wight that species partially succeeds in taking shape, when at St. Jean de Luz, it entirely succeeds but only locally, and on the Mediterranean shores it fully succeeds on a large scale.

Then we see that, if the *local* conditions tend to produce certain forms, the *general* conditions intervene to select among these forms the ones whose success is compatible with the general climate of the region.

So geographical isolation is not necessary for the separation of distinct species of *Patellas*. But, of course, where geographical isolation exists, it certainly favours the natural tendency of the *Patellas* to split into several species.

As we have said, each locality of the Biscayan coast tends to produce a particular form, variety or potential species. It is very likely that, if each of these localities happened to be geographically isolated, the variation special to it would be freer to develop, being no longer held back by the mass arrivals from the neighbouring localities, but only occasionally by difficult infiltrations*. In these conditions, the formation of varieties or distinct species would be necessarily facilitated or at least accelerated. It seems to me that this gives us a very likely representation of the fashion in which the distinct varieties and species of the Macaronesian archipelagos have been formed.

In the Macaronesian archipelagos (the Azores, Madeira, the Canary Isles, the Cape Verde Isles) are found numerous forms of *Patellas*, which all belong to the section *Patella* *sensu stricto* (Pilsbry). This section, except for one Australian species, is proper to the East Atlantic. As there are no *Patellas* on the Atlantic coasts of North America nor in the West Indies,

* The *Patellas* live as planktonic larvae for only a few days: they remain confined to the coastal waters, and they are not found in the open sea (see M. V. Lebour, 1933 and 1935).

there is no doubt that all the Macaronesian limpets have the same origin as the other European-African limpets.

In fact, one can find in these archipelagos *Patellas* belonging to our species (such as *P. lusitanica* and *P. caerulea* at Madeira). But numerous other species have been described as special to these archipelagos.

It is difficult to decide which among them are justified and which are not, as long as we have not made large investigations on the field, and as long as we have not studied the radula in addition to the other characteristics. Meanwhile, we can only rely on the opinion of Pilsbry, who is the author of the last revision of the genus (1891). This attitude seems to me to be all the more reasonable, since Pilsbry has been a great lumpner in the matter of *Patellas*. He even had the idea of a possible reunion between *P. caerulea* Linn. and *P. vulgata* Linn.

Among the species described from Macaronesia, Pilsbry has placed some in synonymy; he has brought others to the rank of varieties, in particular such as *P. crenata* d'Orb. from the Canaries and *P. Loweii* d'Orb. that he considers as varieties of *P. caerulea*, or *P. Baudonii* Drouet from the Azores, which he says is very near to *P. ferruginea* Gmel. Also six other forms are kept by him as distinct species. They are: *P. Moreleti* Drouet (Azores); *P. Gomesii* Drouet (Azores); *P. Candei* d'Orb. (Canaries); *P. citrullus* Gould (Madeira); *P. guttata* d'Orb. (Canaries); *P. rangiana* Rochebr. (Cape Verde Isles).

Although Pilsbry says (1891, p. 81) that these species are still in need of revision, I think that at least some of them have been rightly kept by him.

If we admit that the Macaronesian archipelagos are the last remnants of a lost continental area, we shall find ourselves in the case imagined further back (in reference to the Biscayan coast): the rupture of the continuity of the coast-line, the rarification of the arrival of other *Patellas*, have favoured the natural tendency of the group to give particular forms in external conditions not identical to those of other regions.

If we admit that these archipelagos owe their formation only to volcanic elevation, the role of isolation and of environment would be the same and it operates on stocks formed by occasional arrivals from Europe or Africa. There where these stocks have been able to form a syngameon, which seems to be the case at least in the Azores, the polyvalent variability liberally worked out has been able to give rise to particular types meriting special names.

As to deciding the real taxonomic value of these particular types, I am not able to do so at the present moment, even less than for the types of our coasts which I have nevertheless examined at leisure. Besides, I consider that at present

it would be more harmful than useful to attempt to draw taxonomic conclusions from this work. We must leave the question open for further researches.

May I not then draw a conclusion of any sort? Yes, for methodical order. I firmly insist upon the necessity for extensive study in the field. If, in the study of exotic fauna and flora, we must often, by strict necessity, give ourselves to a work of classification, of arrangement, where our own judgment plays an important part, against this, when we study fauna and flora of our own regions (where practically all recognizable forms have been labelled), we must take on again the mentality of the biologist. We must study very extensively in the field on one side, as geneticists on the other (when possible), in order to benefit most from the control of the facts. And we must do so, not so much in order to decide upon a way of classification, as to force ourselves above all to penetrate into the real nature of the separations or connections which we see before our eyes.

I do not forget that for a long time this mentality is already developed in various branches of natural science, and that it has been praised by many authors. But it is not possible to insist too much upon it, principally in our time, when scientific institutes multiply in the most diverse corners of the globe, and must render possible a great development in this kind of research.

SUMMARY.

The question of systematics and the geographical question are closely linked together in the case of North Atlantic Patellas. These limpets belong to one vast syngameon (large species?) capable of splitting into several species, morphologically and ecologically distinct. This splitting is realized in certain districts of the coast-line (there are no hybrids there despite overlapping habitats), but not in other districts. In these last districts there is much variation, leading to unaccustomed types, each special to a locality. Those divergent types are potential species, as shown by *Patella caerulea* (partially taking shape at the Isle of Wight, succeeding, but only locally, on the Biscayan coast, and fully succeeding in the Mediterranean). So the geographical isolation is not necessary for the formation of new species of Patellas; but, of course, the natural tendency of the complex to split into particular types is greatly favoured where geographical isolation happens, as it is not held back by the arrivals from other localities. Thus we have a concrete representation of the manner in which have been formed the distinct varieties and species of the Macaronesian archipelagos.

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SOME PROBLEMS OF GEOGRAPHICAL VARIATION AND SPECIES-FORMATION.

BY DR. BERNHARD RENSCH (Münster).

SINCE the publication of Darwin's 'Origin of species' geographical races are considered to be the first steps towards new species. Within the last ten or twenty years only some biologists began to doubt this commonly held opinion. J. Philpitschenko (1927), L. S. Berg (1926), D. Rosa (1931), R. Goldschmidt (1935), and especially some palaeontologists supposed that the transformation of species is governed by special laws, whereas geographical races only result from a secondary splitting up of species. It is therefore necessary *to examine, first of all, if it is proved that geographical isolation of larger populations is not only the first step towards new races, but also towards new species, and that such a differentiation also gives rise to higher systematic categories.*

We nowadays know that all animals and plants show mutation and that this process of mutation is a steady one, that it is proportional to time, and that only the degree of mutability of the single genes and their fitness is different. If therefore a larger population becomes isolated, there will always be the possibility that in the course of time it will be altered by the accumulation of mutations and that it will thus become a distinct geographical race. For example: all the little fragments of islands surrounding the Balearic Islands, which were probably separated by the postglacial rising of the sea-level, have different races of lizards, which are widely specialized in colour, size, proportions, shape of scales, speed of locomotion, etc.

Now the isolation does not need to be an absolute one, as is the case on islands. In a larger territory as well the single populations are *relatively isolated*, so far as the animal in question is bound to its habitat, as is nearly always the case, even among birds. Then the isolating factor is not the impossibility of colonizing the adjacent territory, but the fact that these territories are already occupied by the same

species. For that reason such a continuous distribution too gives rise to geographical races, but such races are often connected by gradual transitions, as most of the continental mammals, birds, insects, etc., show. Fairly often such a gradual alteration of the inherited characters takes place that it is nearly impossible to clear up the limit of each race (examples : central European races of tits like *Sitta europaea*, *Parus atricapillus*, etc.). Comparing the races of such species from more distant countries, perhaps from France and Finland, we see that the differences are not less than those between island races, that is to say : it makes little difference whether an inhabited territory separates them, or other populations of the same species.

The number of races which are linked in geographical succession is often quite large. Many complexes of races, or 'Rassenkreise' * as I have called them, of birds, mammals, and insects, which are distributed from western Europe to south-eastern Asia, contain some 20 or 30 races. These large 'Rassenkreise' are of decisive importance to the question of whether geographical variation only gives rise to new races, or likewise to new species. In the time of Darwin most of these geographical representatives were looked upon as species. The discovery of uniting transition forms was considered to be a proof of the change of one species into another. But nowadays nearly all such geographical representatives are only looked upon as geographical races. But now the geographical extremes of large 'Rassenkreise' are very distinct. Races of birds of the same Rassenkreis, from Europe and from south-eastern Asia, for instance, often not only differ in colour and size, but also in osteological characters, in the relative length of feathers, in voice, in number of eggs, in the instinct of migration, etc. That is to say : *the characters by which the races are distinguished are of the same kind as the characters which separate 'valid' species living side by side.* The same holds good with regard to the large Rassenkreise of insects. Geographically extreme races of butterflies, for instance, are not only characterized by size and colour, but also by the duration of development of the caterpillars, by the time of hibernation, and especially by the important structure of the genital armatures. As K. Jordan (1905) pointed out, the differences of the latter organs are sometimes of such a degree that it is hardly conceivable that the extreme races could copulate with one another.

We may, therefore, suggest that extreme geographical races of the same Rassenkreis have reached the same degree of differentiation as 'valid species'. In some cases this assumption is confirmed by the behaviour of such extreme forms.

* A possible translation is 'complexes of races'.

Thus the Great Tit-mouse (*Parus major*) forms a large chain of races, which gradually leads from the European race (green above) through the Asiatic mountain races (without lipochrome) to the races of eastern Asia (*minor*-group with little lipochrome). Now in postglacial times the European race spread eastwards along the inner-Asiatic forest-zone and met the eastern race *P. m. wladivostocensis* in the central Amur region. But no hybridization took place here: both races are living together side by side like two 'valid species' (Stegmann 1931). We have reason to suppose that it is not a strong physiological difference which prevents interbreeding (otherwise at least single perhaps infertile hybrids would be produced), but that psychic factors (the different shape) were decisive. As regards the definition of the species or of the 'Rassenkreis' (compare Rensch 1934*a*) we learn by this that it is not the main consideration that two forms can hybridize fertily, but only that de facto an interbreeding does not happen.

There are some more cases in which it is difficult to decide whether they still are to be looked at as races or already as species. I only want to mention the Shrikes *Lanius collurio* and *L. cristatus*. These two 'Rassenkreise' representing one another geographically on the whole, often mingle in the boundary region in south-eastern Siberia and in Mongolia, but to a great extent they are found living unmixed side by side. And it is to be expected that the very distinct geographical races of some insects too (races of the European beetle *Carabus monilis* or of the African butterfly *Salamis parnassus*, for example) cannot copulate with one another, because they differ too much in size, and especially in the armature of the genital organs. Hence this means: geographical variation does not only lead to new races, but in many cases to new species as well. The terminal links of a large Rassenkreis therefore also may be called species. This fact chiefly induced me to abandon—at least in such cases—the term 'species' and to speak of 'Rassenkreise'.

Moreover, there are a number of intermediate cases between race and species, proving that geographical isolation really leads to valid species. Above all, we have to mention some island forms representing one another geographically which already differ so strongly that we are right in treating them as species. Of hundreds of existing examples I want only to mention the Fruit-Pigeons of the *Ptilionopus porphyraceus*-group in the Australian and South Sea-region, the members of the otter subgenus *Lutra*, which have developed their own 'Rassenkreise' in Europe and Asia, in Africa, and in America, all of them representing one another geographically (compare Rensch 1933, 1934).

Thus we really may claim that geographical isolation leads to new species and at the most we could doubt whether species which have developed in such a manner can gradually produce higher categories too, such as genera, families, and so on—hence, *whether the problem of species-formation at the same time represents the chief problem of evolution*, as Darwin suggested.

In this respect we may state, above all, that mutation steadily occurs, that new species therefore will continue to change (setting aside the relatively rare permanent types which either are scarcely subjected to mutation or which are always selected in the same manner). But the cessation of sexual affinity will no more limit the distribution of neighbouring closely-related forms (former races): the habitats of the new species can now overlap each other, as is shown especially by the young European races in Central Europe returning from their glacial refuges in western and south-eastern Europe (for example: the tree creepers *Certhia brachydactyla* and *C. familiaris*, the Goldcrests *Regulus ignicapillus* and *R. regulus*; the Toads *Bombina variegata* and *B. bombina* etc.).

If we now compare the *characters distinguishing subgenera and genera*, we may generally state that they are of the same kind as the *characters distinguishing species*. The degree of distinctness is only a more marked one. Therefore on this account alone we need not suppose another type of differentiation in the higher categories.

Palaeontological research, however, has shown that there still exist *some special laws of evolution*, which will become evident only by studying larger lines of descent. I will restrict myself to three rules of this kind. (1) The evolution of single groups ordinarily begins with an explosive splitting up into many forms, which later on decreases successively. (2) The lines of descent generally begin with small types and die out with giant or excessive forms (rule of Cope and D  p  r  t). (3) In some cases gradual alterations of characters take place during evolutionary time (orthogenetic rows) which seem to be the result of an internal impetus. I am sorry that there is not time enough to discuss in detail these important rules. Hence I must confine myself to brief outlines.

1. Hitherto existing genetical research teaches that the mutation is steady. When a new type of animal comes into existence, there are in the first instance a number of different habitats at its disposal. New varieties are able to conquer the most different habitats, that is to say: the new type can split up explosively. But in the same proportion as the habitats become occupied by forms of the new type, natural selection will get stronger owing to competition: continually less place will be at the disposal of the new forms.

A complete absorption of all habitats being attained, the production of new forms must stop in spite of continual mutation.

2. As W. E. Castle (1932) and others have already emphasized, there will always exist a higher probability that the larger varieties among the offspring of an animal will enjoy better prenatal and postnatal selection than smaller ones. This fact, however, automatically causes an increase of average size in the lines of descent. So far as the phylogenetic increase of size took place in the northern hemisphere during the tertiary period, climatic selection too can be supposed (rule of Bergmann, Rensch 1924, see below). And the fact that many lines of descent end with giant forms is finally caused too by the impossibility of adaptation to new conditions as contrasted with small forms.

3. Orthogenetic lines of descent are sufficiently explained by the fundamental investigations of D'Arcy W. Thompson and J. S. Huxley on heterogonic growth.

Thus we see that *there is no reason to suppose any mysterious internal impetus in the evolution of higher categories*. Mutation and selection are sufficient to explain not only the origin of geographical races and species by geographical isolation but also the further differentiation of the higher taxonomic units.

And finally the origin of important and entirely new organs too does not need other assumptions. But it is impossible to work out this problem in my report. (I only want to mention the evolution of lungs in fishes, which at first resulted from the necessity of adaptation to periodical dryness in the habitat of dipnoeans.)

II. Now it is a question of great importance to what extent the origin of geographical races occurs in Nature—that is to say, whether we are allowed to consider geographical variation as the chief principle of the origin of species. Even in 1928 I was able to show that most of the groups of animals have geographical races, such groups being mammals, birds, reptiles, amphibians, fishes, insects, mites, scorpions, crayfishes, molluscs and tunicates. Then the discussion of such cases led many zoologists to the discovery of geographical variation in additional groups of animals such as spiders, trematodes, corals, sponges and protozoa. We are therefore justified in saying that *an evolution of species by geographical variation is possible in the great majority of groups of animals*.

But to *what extent* does this kind of evolution occur? We can only answer this question with regard to those few well-known groups in which the application of the geographical principle is achieved.

The palaearctic birds are perhaps one of the most carefully treated groups of animals. In 1933 I published a calculation

(Rensch, 1933) on the basis of E. Hartert's comprehensive work (1910-1933) with the following result: there exist 1492 geographical races of singing birds in 325 'Rassenkreisen' besides 197 species not varying geographically—that is to say, only 11.6 per cent. of all described forms appeared not to be links of 'Rassenkreise'. Now it is interesting that these numbers even during the last few years have obviously been changed. Taking into consideration the now published supplements of Hartert's work (elaborated by F. Steinbacher) we here get the following numbers: 1715 geographical races in 363 Rassenkreisen (2-31 races per Rassenkreis, average 4.7 races), besides only 153 species not varying geographically—that is to say, only 8.2 per cent. of all described forms. Hence among birds evolution by geographical variation may be supposed to be the chief type of evolution.

Palaeartic mammals have not yet been worked out so well. A corresponding calculation of the mammals of western Europe on the basis of G. S. Miller's catalogue (1912) gave this result (Rensch, 1933): 169 geographical races in 31 Rassenkreise, besides 145 unvarying species—that is, 46.1 per cent. of the described forms. Here too the numbers are more favourable to-day (compare Oekland, 1937): in this region we now know 250 geographical races in 76 Rassenkreisen, and no more than 92 species which do not vary geographically—that is to say, only 27 per cent. of the described forms (and some of these too will become members of Rassenkreise later on, as they represent one another geographically). Similar figures are shown by the European reptiles and amphibians (compare Rensch, 1933). Among insects only a few groups of butterflies have been worked out in a corresponding manner. Counting the forms of butterflies from the Indo-Australian region (compare K. Jordan, H. Fruhstorfer and others, 1927) only 11 per cent. of species which cannot be regarded as members of Rassenkreise are found. And among beetles and other insects, land-snails and fishes we have already so many large Rassenkreise now that we may predict that the remaining species, which do not appear as members of such complexes of races, will at least represent a minority. As now most of the other groups of animals too show geographical variation, at least in some cases, we may suppose that *geographical variation represents the commonest type in the evolution of species*. This assumption becomes strengthened by the fact that in well-known groups the numbers of the above-named forms, which are intermediate between race and species, are rather high (for instance, among the birds of the Lesser Sunda Islands 47 such intermediate cases among 160 Rassenkreise).

If, on the other hand, we now ask in how many cases the first step in the evolution of species was certainly not a geographical race, we must realize that such examples are not very numerous. Sometimes an ecological isolation of a population is perhaps sufficient, as especially among insect races, which specialize in certain feeding plants, or as among races of parasites, which specialize in certain hosts (compare W. H. Thorpe, 1930; A. C. Kinsey, 1929; G. Steiner, 1925, and others). Here too forms occur which are intermediate between races and species in this way (compare A. C. Kinsey, 1929; A. Nalepa, 1917). But on the whole such examples are rather rare, perhaps because among biological races the possibility of hybridizing is much greater than among geographically isolated forms.

Further on we have some cases in which a dominant mutation arises and spreads in such a way that the original form disappears gradually. The sugar-bird, *Coereba saccharina*, for example, has a melanistic mutation which has already spread over a part of its area, namely the Antilles, St. Vincent and Grenada, so that to-day practically no normally-coloured specimen is to be found. Some more examples among birds show the same change (compare E. Stresemann, 1926), and similar cases also occur in other groups of animals, the transformation sometimes being supported by natural selection. *But taken altogether the origin of species without geographical isolation is apparently an isolated phenomenon.* And we are not entitled to suppose a similar origin for all those species which do not vary geographically to-day, for such forms are often rather older ones, and they might have arisen from geographical races. Sometimes, moreover, such species represent other related species geographically or the areas overlap only a little, and this circumstance too makes it probable that once geographical variation was the first step in transformation: for example, the bastard nightingale, *Luscinia luscinia*, is a valid species, but it represents the Rassenkreis of the nightingale, *Luscinia megarhynchos*, both areas overlapping only a little in eastern Germany, Poland, and so on (compare too my objections to the so-called 'schizo-typische Artsplitterung': Rensch, 1933).

III. Regarding thus the evolution of species by geographical variation as the chief type of transformation, the results of the investigations upon the origin and inception of geographical races become very important. First of all we have to consider that there exist different types of inception of geographical races*.

1. In a number of cases the variation is undirected—that is

* Compare B. Rensch, 'Typen der Artbildung' in *Biol. Reviews*, Cambridge Phil. Soc. (in the press).

to say, the special characters owe their origin to undirected mutations, which do not reduce vitality and fertility markedly and which are not selected by external factors. Coloured marks, which distinguish tropical races of birds or butterflies, sculptures of the wing-cases of caraboid beetles, differences of the armatures of the genitals of insects etc. may be quoted as examples.

2. In other cases a selection by certain external, especially climatic, factors is evident. As generally many species of the same area are selected in a similar manner, race-characters arise which run parallel with the selecting external factors. We are therefore able to formulate *climatic rules* concerning the direction of changes among geographic races. I have frequently reported this in a number of publications (compare especially Rensch, 1936), and therefore I may confine myself to giving a short account of the chief results.

The so-called *Bergmann's rule*, which is perhaps investigated best, may be formulated nowadays as follows: within a Rassenkreis of warm-blooded animals the races living in colder climates are generally larger than the races living in warmer regions. This rule was established in 1847 by E. Bergmann as being valid among the species of the same genus. I myself reduced it to the geographical races of a species (or Rassenkreis), and proved it by calculating the percentage of exceptions (comparing only the races of climatically extreme parts of the areas I found about 10–30 per cent. of exceptions).

In some cases it was possible to prove exactly that these differences in size are inherited (for example, by F. B. Sumner among races of *Peromyscus*; by A. Ghigi among races of *Numida*). In other cases we can draw the same conclusion from the fact that the gradation of size does not run parallel exactly with the recent climate but with that of the last geological period. Further, I was able to ascertain that the size of cells is the same in European and tropical races of the tree-sparrow (*Passer montanus*) and of the Great Titmouse (*Parus major*), but that the number of cells is different: hence only the rate of cell-division is altered. And from A. Svilha's (1935) measurements on *Peromyscus* we can conclude that the rate of successive divisions is accelerated in larger races.

As E. Bergmann has already stated, this rule seems to have its origin in the fact that the volume of a body increases in the third power but its surface only in the second power—that is to say, a smaller body of a warm-blooded animal has a relatively larger surface than a larger body, and the latter one will better resist cooling off. Hence larger varieties of mammals and birds are pre-adapted for colder regions. But we have to remember that the rule is also observed when a species spread from colder regions to the tropics (small tropic races of *Parus major*,

Acrocephalus arundinaceus etc.). And it is even more difficult to interpret the fact that in some cases, in spite of the influence of climatic differences over thousands of generations, no such selection of size did happen. The wren, *Troglodytes tr. troglodytes*, for instance, has the same size in southern Europe and in northern Scandinavia, although larger races became established on the Shetland Islands and in Iceland.

Quite recently F. Reinig (1938) has tried to show that Bergmann's rule is due to a wrong interpretation, and that there only exists a diminution of size from the centre to the periphery of an area. But he founds his arguments only on single examples, and he assumes unproved ways of expansion. It is easy to disprove his assumption in all those cases in which we exactly know the ways of expansion—for instance, tropic birds like the kingfisher, *Alcedo atthis*, and the oriole, *Oriolus oriolus*, become larger in the European climate (compare my critique in Archiv f. Naturgesch. 1938, in the press).

It is impossible to discuss all the other climatic rules in detail, and I must confine myself to mentioning them only. Allen's rule states: within a Rassenkreis of warm-blooded animals the races living in colder climate have relatively shorter tails, feet, ears and bills than the races living in warmer regions. I think that a number of corresponding examples may be interpreted by heterogonic growth in the sense of J. S. Huxley (1932). But so far as the relative shortening of the above-mentioned organs in colder regions does not run parallel with an increase of body-size we must suppose a selection by climate.

The *rule of the shape of the wing* was formulated by myself during the International Ornithological Congress at Oxford in 1934: within a bird-Rassenkreis the races of cooler regions are ordinarily distinguished from the races of warmer regions by more slender and more pointed wings.

In formulating *Gloger's rule* the fact was noted that within a Rassenkreis of warm-blooded animals the races living in warmer and wetter regions show more pigmentation by melanins than the races of colder and drier regions, and that furthermore in hot and dry zones the light brown melanins prevail, which inversely diminish in cold regions.

The *hair-rule* was formulated by me as follows: within a mammal-Rassenkreis the races living in warmer zones generally have shorter and relatively broader arista-hairs and less wool-hair than races of colder regions.

The *egg-rule* states: within a bird-Rassenkreis the races of colder regions generally have more eggs per clutch than the races of warmer zones. A corresponding *rule of the litter-size of mammals* is not yet sufficiently founded (Rensch, 1936).

I likewise established similar rules concerning size and relative thickness of the shells of land-snails (Rensch, 1932).

At first sight all these rules give the impression that there is a direct influence of climate on the origin of hereditary race-characters, and I myself formerly (especially 1929) supported such an opinion. But meanwhile geneticists have been able to make it seem probable that practically all genes are pleiotropic ones, that hence a selection always can affect unknown characters, which are caused by the same gene as the characters showing climatic parallelism. I therefore assume that we now must endeavour to confine our interpretation to mutation and selection (Jollos' discovery of directed mutation is not verified by Plough and Ives). The importance of such rules of climatic parallelism of characters may be seen in the fact that we get an insight into the laws of race-formation, an insight which *enables us to predict with a probability of 70-90 per cent. how size, proportions, shape of wings, length of hair, colour, number of eggs, etc. must be developed in a certain climate.*

Ladies and gentlemen, the short time only permits me to give a general view of a few of the problems of geographical isolation. For more detailed argumentation I refer to my above-quoted publications. Summing up, we may state: (1) that geographical isolation leads not only to new races, but also to new species; (2) that geographical variation is a chief principle in the evolution of species; (3) that we need not suppose other principles of differentiation for the evolution of higher systematic categories; and (4) that besides an undirected geographical variation we can state a climatic parallelism among geographical races, the causal analysis of which is started by the formulation of, and by the inquiry into, a number of climatic rules.

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GEOGRAPHICAL ISOLATION AS A FACTOR IN SPECIES FORMATION, AND ITS RELATION TO CERTAIN INSULAR FLORAS.

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MANY Linnaean species cover a wide geographical range, especially in a W.-E. direction. Within their area conditions are never quite homogeneous, and many cases are known where the climate is maritime at one end and continental at the other. Such species are, probably with few exceptions, polymorphous; there are extreme and intermediate varieties, sometimes regarded as of specific value. Such forms may or may not correspond to ecotypes, adapted to the special conditions under which they live. I say this without denying that every plant must be adapted to its *milieu*, otherwise it could not exist and propagate itself; but it does not necessarily show any distinctive characters to be explained as a response to the habitat.

We regard a wide-ranging, polymorphous species as a population composed of various genetic combinations; sometimes only a genetic analysis will reveal their differences, in other cases their phenotypic appearance makes them at once distinguishable to the taxonomist. Should the distribution of the population be discontinuous—whether from secondary gaps due to geographical factors or from overland or oversea colonization by a well-marked combination—and should no interbreeding occur or interbreeding is, at any rate, reduced to a minimum, the old collective species splits up into vicarious units. On the other hand, there are many instances where the taxonomist has found it impossible to point out any tangible difference between populations living far apart and, as far as we are able to judge, at present quite isolated from each other (as is the case with many plants common to the Scandinavian mountains and the European Alps), in spite of the general tendency among taxonomists to split up, through critical research, such widely distributed species, a process largely stimulated by a precise knowledge of the area of each unit. If these areas are separated from each other, isolation is made responsible for the existence of well-defined segregates.

Archipelagoes may be expected to furnish evidence of the influence of isolation on the formation of species; and the circumstance that I have occupied myself with a systematic study of insular floras has served, I dare say, as the cause of an invitation to speak on this occasion.

I cannot tell when the idea of isolation as a creative factor was originally conceived, but nothing could have been more

stimulating than Darwin's discovery of the finches in the Galapagos islands, where local endemism is obvious in both plants and animals. Aided at that time by the theory of natural selection and of its different action under different conditions, the creation of species under isolation appeared to be easily explained and an important mode of species-formation. Mutation, selection, extinction, and survival, a process going on undisturbed for a long time was thought to give birth to whole floras or faunas, originating from a single ancestor. This view is set forth also in quite recent works, where no attention is paid to the experimental results of modern genetical science. It used to be a quite simple thing to account for the evolution of endemic floras and faunas in remote islands; oversea immigrants lost, as it were, their balance under the new conditions and began to mutate, different mutants becoming isolated in different islands.

In the light of modern science these theories have lost most of their ground, and we have to look for other reasons for the segregation. I shall not dwell upon the problems connected with oversea long distance dispersal, which have proved to be much more complicated than people thought fifty years ago—the actual distribution of species is certainly not in accordance with the older views,—nor shall I discuss the question of insular endemics and environment. My object is only to cast a glance on one or two systematically fairly well-known insular floras offering examples of local endemism in the form of vicarious species in a restricted sense, originating from a polymorphous population and isolated through the breaking up of a large island, transforming it into an archipelago where different islands are inhabited by different but closely related forms.

The Juan Fernandez islands, two in number, are a classical example of an isolated group; Masatierra, the larger of the two, lies 360 miles off the coast of South America, Masafuera is situated some 90 miles further west, so that they are also widely separated from each other, making local isolation very effective. At the west end of Masatierra is the small and very dry islet Santa Clara, detached from the main island in recent times. We have every reason to believe that these islands represent volcanic strata resting on a submerged land area, which supports also the Desventurada islands farther north, and can be traced a long distance in this direction, and perhaps towards the NW.; an early connection with the continent in a SE. direction seems probable. Isolation is accentuated by the profound difference in climate between the islands and the opposite coast, and the current works in the same direction. Endemism is very high; there are a number of endemic genera with no affinity at all with the present flora

of Chile ; otherwise relations are more with the southern part of that country, where the climate is more like the insular one. Local endemism is very pronounced ; in the case of the flowering plants the rule is that the two islands are inhabited by different species of the same genus. In most cases, however, we can speak of vicarious species only in a broad sense, as they are so unlike each other that they defy all discussion as to their origin ; in many cases we cannot even speak of a *pair* of species or a group of closely related species ; *Eryngium*, *Solanum*, *Wahlenbergia*, *Bromus*, etc. afford some examples, whereas we might speak of a *pair* in such instances as *Peperomia* (*margaritifera*-*Skottsbergii*), or *Gunnera* (*peltata*-*Masafueræ*). *Myrceugenia fernandeziana* and *Schulzei* do not constitute a *pair*, because they belong to different subsections ; still, as forest-trees, they replace each other. Only the following cases suggest a segregation within a common ancestral stock. We have three species of woody *Chenopodium*, belonging to an endemic section, *Ch. Crusoanum* in Masatierra, the closely related *Ch. Sanctæ-Clarae* in Santa Clara, and *Ch. nesodendron* in Masafuera, but it is interesting to observe that this species differs considerably from the two other species. Of *Spergularia confertiflora*, a Chilean species, also found on San Felix island, Masafuera has produced an endemic and well-marked variety or subspecies, constant under cultivation. *Sophora* sect. *Edwardsia* is represented by two closely related species differing from all others in the unwinged pod ; *E. fernandeziana* (Masatierra) is slightly variable. The Rutaceous *Fagara* forms a small but very distinct insular section with *F. mayu* in Masatierra, and the very similar but undoubtedly distinct *F. externa* in Masafuera. The same is the case with *Berberis*. *Halorrhagis* has one species in Masatierra and two in Masafuera, all constant under cultivation. Just as *Sophora*, they are of particular interest. Until I showed that it does not occur there, but is represented by three endemic species, *H. erecta* was quoted for Juan Fernandez ; and being a New Zealand species with no intermediate station it used to be cited as a very good example of long distance oversea migration.

In the endemic genus *Robinsonia* we find, in addition to several species found only in Masatierra, one *pair*, *R. evenia* in Masatierra and *R. Masafueræ* in Masafuera. Of *Dendroseris*, all three subgenera offer examples of the same kind. *D. micrantha*, a common inland species in Masatierra, is represented by *D. pruinata* on the coast-rocks and on Santa Clara ; *D. marginata* and *macrantha* are rare and very local species in Masatierra, represented by *D. litoralis* on Santa Clara and on a small conical rock off the coast of Masatierra ; in this case we have a fourth and more distinct species, *D. macrophylla* on Masafuera (compare *Chenopodium* above !). Further, the

pair *D. pinnata* (Masatierra) and *D. regia* (Masafuera) may be quoted.

The examples given above show (1) that we have a number of cases where different local species are supposed to have originated from a common ancestral stock; (2) that where we have three vicarious species in the three islands, those inhabiting Masatierra and Santa Clara are more nearly related to each other than to the endemic species in Masafuera—a fact that may have something to do with the geographical position.

The Hawaiian flora, famous for its unusual degree of endemism (almost 90 per cent. of the phanerogams), is also renowned for its high number of polymorphic and 'critical' genera, illustrating what used to be called 'progressive' endemism. It should prove an excellent field for genetical research; as it is, we cannot hope to arrive at definite conclusions regarding the history of polymorphism.

No genus appears to be more puzzling than the palm genus *Pritchardia*, which has very few species outside Hawaii, where over thirty, with some varieties, have been recognized. In their mode of occurrence they offer a case parallel, on a small scale, to that of the land-shells. No species is found in more than one island; as there are eight islands with *Pritchardia*, some are inhabited by more than one species. Oahu alone has nine, each found in a separate valley. As a rule there is a single groove or very few groves. The drupes, small to large and apparently unattractive, drop to the ground close to the tree, and barely manage to maintain the species. I remember one particular case where there was a small grove of one species on an almost perpendicular wall; on the other side of the narrow crest was another grove, formed by a different species. External conditions may have been different before the arrival of man, and particularly before the ground was cleared of the lower forests to give room for cane and pineapple plantations; but we have little reason to assume that the palms were less local than at present, even if they were more plentiful in their respective islands and valleys. All the species are closely related. They are tomentose to glabrous, the drupes are large to small, globular to ovoid, and so forth, the characters being combined in various ways, but no hybrids have been described. The *Pritchardia* assemblage suggests an ancestral population which has split up in a number of segregates under isolation. It is generally believed that the archipelago once formed one continuous land.

It is easy to pick out many other genera where the situation is, more or less, the same, with local species and local varieties. Some of these genera were studied by me, others by other monographers. Unfortunately, few if any efforts have been made to trace the history of these genera, and among the

endless descriptions of varieties, forms, and supposed hybrids we lose our bearings completely. In some instances the lines of evolution are somewhat clearer.

The genus *Scaevola* is very diversified in the Hawaiian islands. Besides a number of species which do not interest us here we have three (*Sc. Gaudichaudiana*, *Chamissoniana*, and *procera*) all found in more than one island (then on two neighbouring islands), but hardly ever in quite identical forms and not even presenting a quite homogeneous aspect in one and the same island. To a certain extent they overlap, but no conscientious taxonomist would unite them. Each group of forms presents the picture of units segregated under isolation, which is more or less complete. Similar cases are offered by *Vaccinium* and *Santalum*. *Vaccinium* shows one widespread and somewhat variable species and besides a number of local more or less well-defined segregates regarded as species; in some cases they may be equal to ecotypes, and isolation is, according to my belief, an important factor. The common Oahu Sandalwood, *S. Freycinetianum*, which formed the main source of wealth in the days of the Kamehamehas, is a variable species both in the shape of the leaves and in the length of the corolla and disc lobes; we find in one case a grove of trees with a short, in another with a long, corolla, but careful measurements have shown that they overlap. In Kauai no true *S. Freycinetianum* occurs, but a vicarious species known as *S. pyrularium* with longer corolla and disc lobes and a larger drupe. It is readily assumed that this is an extreme form that happened to become isolated in Kauai. I have seen a plant from the Waianae mountains in Oahu that comes very near *S. pyrularium*. The two species *S. cuneatum* and *ellipticum*, the former generally distributed, the latter very local, have recently been united into one polymorphic species; still, when typical, they appear to be quite distinct.

Of other genera where local endemism occurs, suggesting segregation of different gene-combinations, the following may be quoted:—*Schiedea*, *Geranium*, *Hibiscus*, *Pelea*, *Fagara*, *Acacia*, *Sanicula*, *Cheirodendron*, *Tetraplasandra*, *Labordia*, *Cyrtandra*, *Plantago*, *Wikstroemia*, *Euphorbia*, *Pipturus*, *Astelia*, *Dianella*, *Panicum*, *Deschampsia*, and probably many more, particularly among the Rubiaceae, Lobeliaceae, and Compositae. Two genera deserve special attention, *Metrosideros* and *Bidens*. The former with its bewildering multitude of forms, showing all possible combinations of leaf-shape, hairiness, and flower colour, reminds us of the genus *Rosa*, the latter of *Alchemilla* or *Taraxacum*. Local endemism is very obvious in *Bidens*, whereas *Metrosideros* has not at all been sufficiently studied.

Even with the scanty information that we have to-day,

it is quite evident that the Hawaiian islands offer good opportunities for a study of isolation as a factor in species-formation. This does not imply that isolation in itself would possess any creative power. In most cases it is supposed to be combined with a change of environment, and thus it should favour certain combinations, whereas others cannot be realized. Species limits are thus drawn closer.

The explanation of vicarious units in the two cases mentioned above, Juan Fernandez and Hawaii, is in accordance with the theory that isolation originated through submergence and formation of more or less unsurmountable barriers. Another question is how far we are allowed to stretch this point. There are many instances in the Polynesian region where only few authors have dared to alter the balance between land and sea at a period late enough to have any bearing upon the distribution of life of to-day. Let us return to the Sandalwoods. We find in east and south-east Polynesia a small number of Sandalwoods (on which I have just published a paper), one variable species, *Santalum insulare*, originally described from Tahiti, and also occurring on Raiatea, and represented by slightly different varieties in Marquesas and Raivavae of Austral islands, with a somewhat more distinct variety in Rapa; further, a closely related species, *S. hendersonense*, in Henderson Island. Together with the extinct *S. fernandezianum* of Juan Fernandez which, however, stands apart from the rest, they form the subgenus I called *Polynesica*. Does or does not this assemblage suggest former land-connections? Are the species scattered survivors of a more widely distributed population? Anybody would shrink from drawing far-reaching conclusions from a single example. But many more could be given.

Finally, one more instance will be cited, likely to lead us on to still more unsafe ground. No doubt you are familiar with a small tree often seen in a cold house or even in the open where the climate is mild: *Sophora* or *Edwardsia tetraptera*. It is quoted from a considerable number of stations scattered all around the Antarctic continent. If you look into the matter you will discover that it consists of at least as many subspecies or species as there are stations. They occur in South Chile, Masatierra, Masafuera, Easter Island, Raivavae, Rapa, Chatham Island, New Zealand, Lord Howe's Island, Réunion, and Gough Island—thereby we have completed the circuit of the globe. In New Zealand are several well-marked forms, one in each of the other localities as enumerated here. As long as we counted with a single species it was easy enough to say that it had travelled round the world from some centre, presumably New Zealand, as an oversea emigrant, although the *Sophoras* are not seaside species in the true sense

of the word. What is their history? Are they all to be derived from a population once inhabiting New Zealand more complex than the present one? Did various forms of this population reach each a different island, each on account of changes in the ancestral stock such as cannot now be identified in the present New Zealand species or varieties? Or did New Zealand stock only the nearest island, the next becoming colonized from this, and so forth, and every time a *Sophora* 'germ' arrived at a new place it developed into something new? Or? . . . I guess we can vary the possibilities and suggest other alternatives. Or does the present taxonomic status and distribution bear witness of former land-connections offering an example of the same kind as spoken of above, only on a much larger scale? It is hard to tell which of these theories should appear less objectionable to a critical mind than the others.

Working as we are along regular old-fashioned taxonomic lines, we are likely to get stuck. We must look for assistance from cytology and genetics, but, unfortunately, our material in this particular case consists mainly of woody species, technically difficult to deal with, so that results will be obtained only after many years. The Hawaiian islands would be the proper place for an experimental garden. Their flora is rich, and includes many polymorphous species, local endemism is encountered everywhere, isolation is often perfect. Under such circumstances we ought to arrive at results of a general character, shedding new light upon the question of geographical isolation as a factor in species formation.

The thanks of the Society having been accorded to the various speakers, the PRESIDENT called upon them, if they so desired, to add to their remarks or to reply to points raised by the other speakers.

Dr. JULIAN S. HUXLEY: There are, Mr. President, one or two small points I should like to make. I was much interested in Professor Buxton's remarks as to competition, but I confess that I do not altogether agree with him. Surely if you have fewer types and fewer species, there is bound to be less competition in certain aspects, though not necessarily in others. Take, as a human parallel, the entertainment industry. In my young days the theatre reigned unchallenged. The additional competition produced by the rise of cinema and wireless and, now, television, has surely had its effect? There has been additional pressure, perhaps not on individual members of the dramatic profession, but on the dramatic profession as a whole, and we do not any longer get certain aspects of

drama provided. Such an analogy would apply between a number of species.

A good example in the British Isles is that of the hare. The hare found in Ireland is the mountain hare of Great Britain. The common hare, derived from eastern Europe, did not succeed in reaching Ireland. In Ireland, the mountain hare is able to do what it cannot do in Great Britain; it is able to range over the lowlands as well as the highlands. In Great Britain the mountain hare is subjected to additional competition and, as a result, to restriction of range and habitat.

As to Professor Skottsberg's remark that we are not acquainted with Juan Fernandez island, this was, after all, the home of Robinson Crusoe, and if only he had had a woman with him instead of Man Friday we might have seen another example of geographical differentiation as the result of isolation!

Professor P. A. BUXTON: I only wish to deal with a point that Professor Huxley has just raised about the difference in competition between faunas on oceanic islands and in continental areas. I cannot accept the simple general view that in the islands competition is less than in the continents. In many ways perhaps there is less competition on an island, though in other ways the difference does not exist. I wanted rather to raise doubts than to preach any dogma in the matter.

Dr. E. FISCHER-PIETTE: In reply to Professor Huxley I may say that, judging from the first results, there are several summits in the curve, each one corresponding to one species, so far as the length of the radula ribbon is concerned. But the question is to be further investigated on a larger number of specimens.

Dr. BERNHARD RENSCH: I have only to emphasize that in former days it was usual to say that isolation had no creative power, as Professor Skottsberg told us. Now we know that mutation is a steady process, proportionate to time, and we may say that it has—not verbatim, but de facto—a creative power.

Dr. C. SKOTTSBERG replied to Dr. Rensch: I think you have misunderstood me. Isolation is not the creative factor, but it sets to work factors which may lead to the origin of new combinations and their maintenance. That is what I wished to say.

CATALOGUE OF THE EXHIBITS IN THE SOCIETY'S
LIBRARY ON THE OCCASION OF THE 150th
ANNIVERSARY CELEBRATIONS.

By S. SAVAGE, F.L.S., Librarian and Assistant Secretary.

SOME PORTRAITS OF LINNAEUS WHICH GIVE A
BETTER IDEA OF HIM DURING HIS WORKING
PERIOD THAN THE LATER PORTRAITS BY
ROSLIN, PASCH AND KRAFFT.

1. Photograph of the original painting by HOFFMAN of
Linnaeus in his Lapland dress. [Ætat. 30.]

Probably gives a good idea of his general appearance at the time it was painted. The extraordinary boots make him look somewhat taller than he really was.

2. Lithograph of J. E. REHN'S drawing of Linnaeus made in
1747. [Ætat. 40.]

This portrait gives a good idea of his general appearance at the time when he was working day and night on his 'Species plantarum'.

3. Engraving by I. M. BERNIGEROTH, 1749, from a drawing
made in 1748. [Ætat. 41.]

This portrait was prefixed to some copies of 'Philosophia botanica', 1751. In one of his autobiographies (written about 1769) Linnaeus states that this is the best portrait of himself.

4. Marble bas-relief by SERGEL made in 1766. [Ætat. 59.]

Sergel, the Swedish sculptor, made at the Swedish Queen's command a marble bas-relief of Linnaeus. In 1794, sixteen years after Linnaeus's death, he executed the medallion on the monument in Uppsala Cathedral.

5. C. F. INLANDER'S medallion, 1773. [Ætat. 66.]

Without any doubt this beautiful medallion gives a true picture of Linnaeus as an old man. Solander considered that it gave a better idea of Linnaeus than any of the paintings. The replica of this medallion, presented by Sir Joseph Banks in 1790, is on the south wall of the Library.

6. SERGEL's medallion on Linnaeus's monument in Uppsala Cathedral, 1794.

Although Sergel had made a bas-relief of Linnaeus in 1766, it is obvious that this later medallion was inspired to some extent by Inlander's medallion.

General note on Linnaeus's personal appearance.

From contemporary records we are able to visualize Linnaeus as a stockily-built man somewhat below middle height: his head large, with a high and prominent back to it; his forehead moderately high, much wrinkled in old age; his face open and pleasant; his eyes bright brown, piercing, full of life and intelligence; of somewhat myopic but excellent sight, capable of examining minutely the smallest object, surrounded in old age with pronounced wrinkles due to the continual muscular contraction necessary in his examination of natural objects. His movements were brisk and lively; and it was his practice never to delay doing anything that could be done at once. From childhood his teeth were bad, and before he was sixty years of age he was toothless. (The asymmetry of the lower part of the face in the Bernieroth engraving is probably due to bad teeth.) At fifty years of age, as the result of several severe illnesses, and his continuous labours, his walk had become less lively and his body somewhat bent forward.

SOME FANCIFUL PORTRAITS OF LINNAEUS.

7. Early childhood of Linnaeus. An engraving from the 'Select Magazine', 1822.

A similar illustration was shown as exhibit No. 50.

8. Lithograph by E. DESMAISONS from a picture by the French painter LOUIS PROSPER ROUX, showing Linnaeus as a very young man resting in his study after his labours.

An entirely imaginary composition!

9. Wood-engraving by G. P. HINDLEY illustrating the story that Linnaeus fell on his knees before a gorse bush on Putney Heath.

Some of Linnaeus's biographers took this story as a myth. The artist, while succeeding in making a good picture, has failed to give a convincing portrait.

PORTRAITS OF SOME OF THE FIRST SEVEN FELLOWS
OF THE LINNEAN SOCIETY OF LONDON, TO-
GETHER WITH SOME OF THE FIFTEEN FELLOWS
MENTIONED IN THE FIRST CHARTER, 1802.

10. (Sir) JAMES EDWARD SMITH, F.R.S., the first President.

Below the portrait is shown the imaginary pursuit by a Swedish man-o'-war of the ship bringing the Linnaean Collections to England.

11. Rev. SAMUEL GOODENOUGH, F.R.S. (Bishop of Carlisle),
the first Treasurer.

12. JONAS DRYANDER, the first Hon. Librarian ; and later
Vice-President.

13. JAMES DICKSON, one of the first seven Fellows.

Water-colour by Wageman, painted in 1822.

14. ALEXANDER MCLEAY, the second Hon. Librarian ; and
later Secretary.

In 1825 he became Colonial Secretary to the Government of
New South Wales.

15. AYLMER BOURKE LAMBERT, Vice-President.

Author of ' Description of the genus *Pinus* ', 1803-24.

16. CHARLES HATCHETT, F.R.S.

Chemist ; co-founder, with Sir Everard Home, of the Animal
Chemistry Society.

17. Dr. THOMAS YOUNG, F.R.S.

Physician, physicist and egyptologist. He rendered valuable
assistance in translating the demotic text of the Rosetta stone.

PHOTOGRAPHS OF SOME OF THE EARLY
HOMES OF THE SOCIETY.

18. No. 12 GREAT MARLBOROUGH STREET.

The meeting-place of the Society from April 1788 to September
1795 The house was James Edward Smith's town house.

19. PANTON SQUARE.

The Society had part of No. 10 Panton Square as its headquarters from 1795 to 1805.

20. No. 9 GERRARD STREET, SOHO.

The Society occupied this building from 1805 until 1821. An interesting letter of J. Dryander concerning this building was also exhibited.

21. No. 32 SOHO SQUARE.

The Society occupied this house for thirty-six years (1821-57). It had been Sir Joseph Banks's town house; it was pulled down last year.

INTERESTING DOCUMENTS FROM THE
LINNEAN SOCIETY'S ARCHIVES.

22. Letter, dated Mechlin, 19 February 1567, from REMBERT DODOENS to Carolus Clusius. (Ward MSS.)

With Clusius's docket on the verso.

23. Letter, dated Leiden, 16 April 1598, from CAROLUS CLUSIUS to Bernardus Paludanus. (Miscell. MSS.)

24. Letter, dated Chiswick, 28 November 1757, from WILLIAM HOGARTH, the painter, to John Ellis. (Ellis MSS.)

Praising an engraving of corallines sent by Ellis. 'As for your pretty little seed cups or vases, they are a sweet confirmation of the pleasure Nature seems to take in superadding an Elegance of form to most of her works, where ever you find em When I have the pleasure of seeing you next we will set down, nay kneel down if you will and admire these things'

- 24 a. Letter, dated 10 July 1788, from LOUIS D'AYEN, Duc de NOAILLES (1713-93), Maréchal de France.

Accepting his election as Hon. Member of the Society. He and Sir Joseph Banks were the first two Hon. Members. A correspondent of Linnaeus and a great lover of horti culture the Duc de Noailles recommended strongly the adoption of the Linnaean System in France. The genus *Ayenia* commemorates him.

25. Recommendation, dated 23 April 1798, for election as F.L.S. of EDWARD JENNER, M.D., of Berkeley, Gloucestershire.

Jenner was elected F.L.S. in the year in which he published his 'Inquiry into the causes and effects of the Variolae Vaccinae . . .'

26. Letter, dated Norwich, 19 July 1807, from (Sir) JAMES EDWARD SMITH to Alex. McLeay.

One of many letters from the first President in the Society's Archives. In this letter Smith refers to the early prestige of the Society: 'we must keep up that authority of the Linn^a Soc^y, which foreigners are ready to allow us, if we do not throw the sceptre from us.'

27. Letter, dated Whitehall, 18 November 1830, from Sir ROBERT PEEL to Lord Stanley, P.L.S.

Conveying the consent of H.M. King William IV to become Patron of the Society.

28. Letters, dated Russell Square, April 1825, from Sir THOS. LAWRENCE, P.R.A., to Alex. McLeay, concerning sittings for the latter's portrait.

29. Letter, dated 35 Gerrard Street, 18 December 1821, from CHARLES KEMBLE, the actor, making enquiries about No. 9 Gerrard Street, which the Linnean Society had just left for No. 32 Soho Square.

30. Letter, dated 3 November 1852, from (Sir) RICHARD OWEN to the Librarian of the Linnean Society.

Introducing 'my friend M^r Lubbock to have access to the Library . . .'. (In all probability this was the future President, Sir John Lubbock, afterwards Lord Avebury.)

31. Letter, dated 3 Spanish Place, 11 May 1842, from Captain F. MARRYAT, the novelist, to J. J. Bennett.

A letter, full of humour, concerning the non-payment of his subscriptions.

32. Letter, dated Barking, E., 3 February 1872, from ALFRED RUSSEL WALLACE to the Secretary of the Linnean Society.

Expressing his thanks for his 'unsolicited election' as F.L.S.

33. Memoranda, dated June 1873, from Canon CHARLES KINGSLEY, F.L.S.

34. Letter, dated Down, 27 May 1881, from CHARLES DARWIN to G. J. Romanes, Sec.L.S.

An interesting letter concerning the painting of the portrait of Darwin in the Society's Meeting Room.

35. Letter, dated 21 Eccleston Square, 16 January [1862], from (Sir) CLEMENTS R. MARKHAM.

Sending some publications, and reporting the success of the introduction of *Cinchona* trees in the Neilgherry Hills.

36. Minute Book showing the record of the FOUNDATION MEETING of The Linnean Society of London held on 26 February 1788.

The minutes are in the handwriting of Thomas Marsham, the first Secretary of the Society. It will be noticed that the Society's name is spelled 'Linnæan', but it was soon altered to Linnean. In the next exhibit Sir James Edward Smith gave his opinion on the matter many years afterwards.

37. Letter, dated 10 March 1810, from Sir JAMES EDWARD SMITH to the Editor of the 'Monthly Magazine', reprinted by Lady Pleasance Smith in the second volume of the 'Memoir and correspondence of the late Sir James Edward Smith' (1832).

In this letter Smith expresses the opinion that the Society's name should have been Linnaean, because Linnaeus was a family name and von Linné a title of honour.

38. The first signatures in the ROLL BOOK OF THE LINNEAN SOCIETY.

Among these signatures is that of John Rotheram, the only English student of Linnaeus.

39. The first SEAL OF THE LINNEAN SOCIETY.

(a) The Die.

(b) Plaster cast made from the die by courtesy of the Department of Coins and Medals, British Museum.

(c) Slightly enlarged photograph of the Plaster cast.

When the Society was granted its Charter, in 1802, this seal was replaced by one bearing the Society's Arms.

40. THE LINNEAN SOCIETY'S COAT-OF-ARMS.

(a) Letters and sketches from the College of Arms.

(b) Sketches made for Linnaeus for the Coat-of-Arms he wished to have, but which was disallowed by the Swedish Herald in favour of one with three Crowns for the three Kingdoms of Nature *.

PERSONAL RELICS OF LINNAEUS AND RELATED EXHIBITS.

41. WALKING-STICK, with a design of *Linnaea borealis* carved on the handle.

The original label of the donor was also exhibited.

42. PENCIL-CASE and a piece of INDIA RUBBER.

43. Some of the WOOD-BLOCKS made to illustrate the 'Campi Elysii' of the elder and younger RUDBECK.

44. ALMANACK for the year 1735, annotated by Linnaeus.

Containing short notes on the interleaves. Against the date of his own birthday Linnaeus has noted, in mirror-writing, his own birthday and similarly against that of his betrothed, Sara Lisa Moraea.

These annotations have been published in Swedish by Holmström (Bot. Not., Dec. 1845), by Ugglä, with commentary (Sv. Linné-Sällsk. Årsskr. xvii, 1935); in German by Beilschmid ('Flora', Feb. 1847); and in English by Wallich (Proc. Linn. Soc. ii, 1848).

* On the inner cover of Linnaeus's copy of the printed volume of Count Tessin's letters, published in 1751, is a slight sketch by Linnaeus combining the two ideas. This sketch, which is circular in form, was probably made in connection with the design for the Tessin Medal of 1758.

45. CARVED RHINOCEROS HORN.

Sent to Linnaeus by Magnus Lagerstroem, of the Swedish East India Company. 'An exquisite specimen of Oriental sculpture, evidently alluding to the mythology of India....' (Smith, 'Exotic Botany', i. p. 61, engraving).

46. LINNAEUS'S ADDRESS whilst in London.

Written on the wrapper of a letter from Boerhaave, whose seal occurs twice. As Linnaeus did not speak English, he no doubt carried this address about with him during his stay in London. Both sides of the leaf contain rough memoranda of his movements in Holland immediately prior to his departure for England.

47. UNUSUAL EARLY SIGNATURE OF LINNAEUS in Sennart's 'Hypomnemata physica...', Francofurti, 1636, and Mylius's 'Hortus philosophicus...', Gorlicii, 1597.

The inscription on the title-page of the first book is 'Carolus Linnaeus 3v 1726'; but that on the fly-page 'Carolus N: Linnaeus 3v'. The initial N stands for his father's Christian name 'Nils'; and the scruple sign stands for daler and shows the price paid for the book. The title-page of the second book has 'Carolus N. Linnaeus. Wexio d: 4 Mart. 1727'; the volume contains a few annotations by Linnaeus.

48. An AUTOBIOGRAPHY of Linnaeus to the year 1734.

This MS. was inserted at the end of his copy of Scheuchzer's 'Agrostographici Idea....' Tiguri, 1719, which bears his signature on the title-page with 'Upsal. 1728'.

49. A LATER AUTOBIOGRAPHY of Linnaeus to about the year 1769: Vita Caroli Linnaei....

A transcript in the handwriting of J. Lindvall, with corrections by Linnaeus.

50. FANCIFUL ENGRAVING of Linnaeus as a boy, in 'Les Enfants studieux', Ed. 4. Paris, 1818. (*Lent by Lady Isabel Browne, F.L.S.*)

EXHIBIT ILLUSTRATING LINNAEUS'S DEVELOPMENT AS A BOTANIST.

51. DE INGRESSU AD BOTANIAM [sic] A DR. ROTHMAN EXHIB.
[late 1726 or early 1727]. [*Ætat.* 19.]

Written on five blank pages of an older MS. on Medicine, this is the earliest example of his botanical writings; the MS. also contains his notes of Dr. J. Rothman's private tuition in Medicine, given to Linnaeus at Wexiö (Växjö) previous to his becoming a student at Lund University in August 1727. On one of the pages exhibited is a series of small drawings illustrating Tournefort's system.

It is evident from this MS. that Vaillant's work on flower-structure was made known to Linnaeus in 1726 or 1727.

(In Swedish and Latin; unpublished.)

52. Annotations and drawings in JOHRENI VADE-MECUM
BOTANICUM, made in 1727-8. [*Ætat.* 20-21.]

Linnaeus's observations on plants during his brief stay at Lund University are entered on the interleaves. The fly-leaves at the beginning contain notes on Tournefort's life and sketches of flowers illustrating his system.

(Partly published by Dr. O. D. Gertz in 1926.)

53. Linnaeus's EARLY ANNOTATION OF A LOCAL FLORA. Inter-
leaved copy of Linder's 'Flora Wiksburgensis . . .',
Stockholm, 1716. [*Ætat.* 21.]

The plants are numbered 1 to 547 and the synonyms of Tournefort, Bauhin and others entered up by Linnaeus.

54. Two early MSS. arranged on Tournefort's system:—
SPOLIA BOTANICA, 1729, and HORTUS UPLANDICUS, 1730.
[*Ætat.* 22-23.]

It is usually stated that in 1729 the reading of a review of S. Vaillant's work on the structure of flowers gave Linnaeus his inspiration to found the Sexual System, but No. 51 of the present Exhibit proves that Vaillant's ideas were known to Linnaeus in 1726 or 1727.

Note the change to the Sexual System in Exhibit No. 56.

(Published.)

55. First draft of *FUNDAMENTA BOTANICA*, Upsaliae, 1730.

[*Ætat.* 23.]

Showing that very early Linnaeus was devoting study to the rules of classification.

56. Early MS. arranged on the Sexual System:—*ADONIS UPLANDICUS*, 1731.

[*Ætat.* 24.]

Facsimile of one of the earliest MSS. in which Linnaeus adopted the Sexual System. Another MS., a rewritten 'Hortus Uplandicus', belongs also to the year 1731.

57. FIRST APPEARANCE OF THE SEXUAL SYSTEM IN PRINT: 'Florula Lapponica' (Acta Soc. Uppsala, 1732, pp. 46-58; 1735, pp. 12-23).

[*Ætat.* 25.]

58. *SYSTEMA NATURÆ*. Ed. 1. Lugduni Batavorum, 1735.

[*Ætat.* 28.]

In this important work, printed two centuries ago at the expense of his friends J. F. Gronovius and Isaac Lawson, Linnaeus as a botanist published his re-arrangement of all known genera according to the Sexual System.

[N.B.—The second edition of this work was exhibited, for reasons of space.]

59. *FLORA LAPPONICA*. Amstelaedami, 1737.

[*Ætat.* 30.]

In this, as in Linnaeus's other botanical works (with one exception) previous to the year 1753, the plants are recorded by lengthy specific diagnostic phrases.

60. Annotations in an interleaved copy of *GENERA PLANTARUM*. Ed. 1. Lugduni Batavorum, 1737.

[*Ætat.* 30-.]

This copy has a MS. title-page written by Linnaeus, changing the title to 'Species Plantarum'. The annotations appear to be Linnaeus's first attempt at the 'Species Plantarum'. Perhaps owing to the fact that this volume has been kept among Linnaeus's printed books, the historical importance of these annotations has been overlooked hitherto. The MS. title-page also bears a note by Linnaeus that he gave this copy to his son in November 1752, when the latter was eleven years of age.

(Unpublished.)

61. Early draft of SPECIES PLANTARUM. c. 1746-8.

[Ætat. 39-41.]

This MS. was assembled by Dr. J. M. Hulth, who published a short account of it in 1912. It deals with about 600 genera, but only in a few instances are the binary names inserted. Its style differs considerably from that finally adopted.

(Unpublished.)

62. LINNAEUS AND CASPAR BAUHIN. Copy of Caspar Bauhin's 'Pinax', ed. 2 (1671), with Linnaeus's determinations written in the margins.

[Ætat. 39-41.]

This copy was in Linnaeus's possession from 1730, and was used to record his early determinations of the genera; later, when working on the 'Species Plantarum', he added his specific names.

63. LINNAEUS AND BURSER'S HERBARIUM. Linnaeus's MS. of his determinations of Burser's plants.

[Ætat. 42-43.]

The herbarium of Joachim Burser (1583-1639), a pupil of Caspar Bauhin, was of much help to Linnaeus in settling the identities of Bauhin's species. The herbarium is still preserved in Uppsala.

(Published in 1937.)

64. Dissertation : PAN SVECICUS. Upsaliae, 1749. [Ætat. 42.]

In this dissertation binary names were published for the first time by Linnaeus. It was concerned with Economic Botany, and gave an account of experiments in relation to Agriculture and the feeding of Cattle. Linnaeus here gave some of his projected binomials a first trial in print.

65. Portion of a late MS. of SPECIES PLANTARUM, 1753.

[Ætat. 46.]

Only a portion of the MS. is preserved. So far as it has been investigated, it would appear not to be a portion of the final MS. of this celebrated work.

66. LINNAEUS AND THE NATURAL SYSTEM. Linnaeus's own copy of 'Philosophia botanica', 1751, showing his copious alterations to his sketch of a Natural System.

At the age of 31, Linnaeus published his *Fragmenta Methodi Naturalis* in 'Classes Plantarum', 1738. With his revision of this in the 'Philosophia botanica', 1751 (pp. 27-36), his interest did not end, as may be seen from his later annotations. Note his deletion of the words 'Natura non facit saltus'.

Further annotations are to be found in two copies of the sixth edition of 'Genera Plantarum', 1764.

67. DISQUISITIO DE QUAESTIONE AB ACAD. IMP. PETROP. 1759
PROPOSITA DE SEXU PLANTARUM

MSS. of portions only of the Swedish and Latin texts. As the Latin text has Linnaeus's corrections, it would seem that he may have dictated this work in Swedish and, after some good Latinist had made the translation, added his final corrections.

68. Linnaeus's annotations on SEXUS, GENUS, SPECIES, SYSTEMATA, written after 1760.

These annotations, occupying four pages, appear to be hurried notes for a lecture or perhaps the dictation of a thesis. The page exhibited showed 37 queries or statements, among which are 'an novæ species possibiles', 'Pleni cur steriles', 'mell [sic] cur in floribus'.

OTHER LINNAEANA

69. LINNAEI MATERIA MEDICA, Liber I, de plantis . . . Holmiae, 1749.

Interleaved copy, very copiously annotated by Linnaeus. On the frontispiece he has written *experte crede fide*. The end fly-leaves contain *Pharmacopœia Holmensis*; Linnaeus has also added his binomials in the margins.

70. EARLY MS. ON INSECTS. *Catalogus plantarum eruciferarum quas annotavit Diligentiss. Goedart in libro suo de insectis in ordinem Tournefort: . . . Mouffetti . . . Listeri . . . exhibitus.* [4 leaves.]

71. LINNAEUS AND ARTEDI. Linnaeus's copy of Artedi's 'Ichthyologia . . . edidit Carolus Linnaeus . . .', Lugduni Batavorum, 1738.

In the margins of this copy Linnaeus has written his binomials. The fly-leaves contain interesting annotations. Those exhibited have an epitaph on Artedi written by A. Celsius and translated into English by G. Shaw, the latter in Sir James Edward Smith's handwriting.

72. ARTEDI'S SIGNATURE in Linnaeus's copy of Majus, 'Physicae veteris et novae . . . synopsis . . .', Francofurti, 1688.

Artedi has signed 'Petrus Arctædi 1729' and also 'A^o 1729. d. 12 April. P.A.'

73. LINNAEUS'S MS. ITER AD HORTUM DEI institutum a Fr. de Sauvages. [3 leaves.]

In this MS. Linnaeus has attempted to reconstruct a picture of the flora of the region near Montpellier formerly known as *Hortus Dei*. He has divided the area into districts and given the plants which he has ascertained to grow there. The chief source of his information appears to have been the numerous letters he received from François de la Croix de Sauvages, professor of medicine at Montpellier; and the date of the composition of the MS. is after 1755.

(Unpublished.)

74. LINNAEUS'S LATER WORK ON THE SWEDISH FLORA. Copy of his 'Flora Svecica . . .', ed. 2, Stockholmiae, 1755.

The fly-pages and additional MS. 'Florae Svecicae Appendix 1773' give some of Linnaeus's last observations on the Swedish flora. On one of the fly-pages is 'Nomina Svecica Veterum Monosyllaba'.

75. LINNAEUS AND ENGLISH PLANT-NAMES.

The list is written on the third and fourth pages of the genus-cover of *Nitraria* in the Linnaean Herbarium.

76. LINNAEUS'S DETERMINATIONS of the plants illustrated in Plukenet's 'Phytographia', 1691-6.

This copy has Olaf Rudbeck's signature on the title-page, and was early in Linnaeus's possession. Note that the generic names were written in at an earlier period than the specific names.

77. SOME OF LINNAEUS'S LAST ANNOTATIONS in an interleaved copy of 'Systema Naturae', ed. 12.

78. LINNAEUS'S LATER METHOD OF KEEPING RECORDS of new species of both plants and animals. Slips measuring 13×7.5 cm.

79. MS. of 'ITER LAPPONICA', together with the original vellum covers.

The covers still contain some leaves of the original MS., and are opened at the page which shows Linnaeus's drawing of the old Lapp woman who befriended him when in difficulties.

80. ONE OF LINNAEUS'S LAST MSS. Descriptions of new animals. About 1775 or later.

The MS. is mainly in the handwriting of an amanuensis. Linnaeus's corrections and additions betray the enfeebled state of his health.

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81. SIX SHEETS FROM THE LINNAEAN HERBARIUM.

(a) LINNAEA BOREALIS.

Not the type-specimen, which is in Gronovius's herbarium in the Department of Botany, British Museum.

(b) ARTEDIA SQUAMATA.

The genus was named to commemorate his friend, Petrus Artedi, who met an early death in Holland by falling into a canal. Linnaeus chose this umbelliferous genus to honour his friend because Artedi had devoted much attention to such plants. The sign written on this sheet means that the plant had been collected by Hasselquist, and has the same meaning as the sign used on sheet (d).

(c) *AMARYLLIS FORMOSISSIMA*.

This sheet is one of the duplicates Linnaeus received from Clifort's herbarium. The engraved 'pot' indicates this.

(d) *JASMINUM GRANDIFLORUM*.

The sign denotes that the plant was collected by Hasselquist.

(e) *VIOLA TRICOLOR*.

Note the excellent preservation of the colour of the flowers.

(f) *MASSONIA LATIFOLIA*.

The genus was named by Linnaeus in honour of the collector, Francis Masson. Linnaeus received this specimen towards the close of his life, and has written, in a somewhat shaky hand, the generic name. The younger Linnaeus added the specific name.

82. ZOOLOGICAL SPECIMENS FROM THE LINNAEAN COLLECTIONS.

(a) A drawer of the INSECTS.

(b) Examples of the MOLLUSCA. (One of the tin boxes used by Linnaeus for his shells was included.)

(c) Linnaeus's ARTIFICIAL PEARLS.

Some of the artificial pearls made by Linnaeus. His method was to insert in small holes made in the shells of freshwater mussels pieces of fine silver wire bearing a small ball of limestone composition, which in time became coated by the matter deposited by the mollusc. The Crown Jeweller examined the pearls so made, and declared them to be as good as natural ones. Linnaeus was voted a large reward for this discovery, but it does not appear that he received it.

83. ZOOLOGICAL SPECIMENS FROM THE LINNAEAN COLLECTIONS.

(a) Carapaces of TORTOISES and TURTLES.

(b) Examples from the Collection of FISHES.

84. THE CHARTERS of the Society, 1802 and 1904, and the GRANT OF ARMS.

OBITUARIES.

RICHARD HENRIK BEAMISH (1862-1938), a prominent business man of Cork, at one time Chairman of the Board of Directors of Beamish and Crawford, Ltd., Brewers, died at Weybridge, Surrey, on 23 February, 1938. He took a leading part in the municipal affairs of Cork. As long ago as 1906 he was High Sheriff. Later he became an Alderman, and was many times a member of the Cork Corporation. When a Parliament was established at Dublin in 1923 he was elected for Cork City and remained a member for four years. During discussions in the Dail he frequently exerted himself in expounding problems on scientific agriculture. He experimented, also, in agriculture on his own land. He left Ireland in 1931, when increasing years told him that he had need to relinquish his activities, both commercial and political. Up to that time he resided at Ashbourne, Glounthane, County Cork, and was the owner of one of the most attractive gardens in Ireland, wherein he had converted an old quarry into an extremely beautiful rock garden stocked with the rarest of plants and made an artificial lake where blue *Nymphaeas* flowered freely. His interest in his rare plants led him to join the Linnean Society in 1916.—R. W. G. HINGSTON.

EDWARD THOMAS BROWNE, who died on 10 December 1937 in his 72nd year, had been a Fellow of the Society for nearly a quarter of a century; he served for two periods on the Council, and from 1920 to 1923 was a Vice-President.

Although he became a renowned authority on the Coelenterates, on which he published many important memoirs, it was not until after he had left Queen's College, Oxford, that he turned to the study of zoology. After graduation he first became interested in microscopy and the study of pond life; and in 1891-2 he took lectures in zoology at University College under Professor Weldon. It was at these lectures that his enthusiasm for marine biology was aroused, and from that time until the close of his life he remained an assiduous student of the Coelenterates. He worked constantly at Plymouth and other marine laboratories, visited many localities in search of material for his work, and organized parties to study the marine fauna of Valentia Island in the south-west of Ireland. His interests were mainly in the natural history and classification of marine animals, and in his work on Hydro-medusae he made every effort to trace their life-histories by rearing them from the Hydroids.

It was his hope that he might one day be able to write a monograph of the British species of Medusae; but in this he was greatly interrupted, for he quickly became an acknowledged authority on the group and many collections from all

parts of the world were sent to him for examination and report. Towards the end of his life he realized that he could not himself complete the monograph; he then made provision for the work to be continued at the Plymouth Laboratory, and in due course a full account, incorporating all the detailed notes which he made during many years of active work, will be published.

Browne wrote a number of papers on the British Coelenterates and the results of many important scientific expeditions include memoirs which he contributed*. As a collector he was highly skilled; he was an accomplished artist and an expert photographer, and he brought to his work very great technical ability. In 1898 he discovered that many marine animals could be kept in a healthy condition by gentle and intermittent agitation of the water, and the apparatus he designed for this purpose, the 'plunger jar', is now part of the standard equipment of every marine laboratory.

After his marriage to Miss Margaret Robinson, whom he had met first many years before at Professor Weldon's lectures, Browne made his home at Berkhamsted, where his friend the late Canon A. M. Norman lived. Here he built himself a laboratory and for many years worked with unabated enthusiasm at the subject of his choice, spending much time in giving advice and assistance to correspondents in all parts of the world. Though he worked slowly, everything he did was characterized by accuracy and extreme thoroughness; he had a passion for orderly method, the books in his large scientific library, his specimens, and his notes were all fully catalogued and available for immediate reference.

Throughout his life he was a staunch supporter of the Marine Biological Association, and the Plymouth Laboratory owes much to his generosity. He will be remembered not only for his numerous benefactions and high reputation as a zoologist, but, by those who knew him, for his power to infect others with his deep love of nature, for his genial outlook on life, and for the help and wise counsel that he so freely gave to all who needed it.

STANLEY KEMP.

WILLIAM JAMES ROLPH DEEKS was educated at the Cambridge and County High School, which he left in 1916 to be gazetted to the Norfolk Regiment. He served through the rest of the War in Egypt and Palestine, and was demobilized with the rank of Captain in 1920. On leaving the Army he returned to Cambridge—to the University—and obtained 2nd class Honours in the Natural Science Tripos, and took up teaching. In his first two schools he had to introduce the subject of

* A list of Browne's papers will be found in *Journ. Marine Biol. Assoc.*, xxii, p. 409 (1938)

Biology, which must have taxed him to the utmost, but the experience stood him in good stead when in 1928 he arrived at the City of London School. There he made himself felt. He reorganized the Biology Laboratories and the teaching; and seems to have lived for nothing else.

His interest in Biology induced him to become a Fellow of the Linnean Society in 1926.

He lived a life of serious enthusiasm for his teaching work, which left him no time for original research. But he was no lesser figure on that account, for he has left behind a high ideal of single-mindedness and efficiency which will not be forgotten by his many grateful pupils. He died on 14 July 1937 from cerebro-spinal meningitis.

D. M. REID.

STANLEY EDWARDS was born at 'Kidbrooke Lodge', Blackheath, 24 May 1864, and died at Harrogate 21 March 1938, thus nearly completing his 74th year. In early life no doubt he was attracted by the varied beauty of the extensive and well-equipped garden attached to his home. Later, as he got older, the natural richness of the neighbourhood in its fauna and flora, a surround hallowed by the records of the late H. T. Stainton, extended the area of attraction. Educated privately and with ample means to supply his pursuit of natural history, he gradually got together a fairly representative collection of British Macro-Lepidoptera and an adequate library for his study.

His father was a member of the firm of Edwards and Edwards, tea-brokers, of Fenchurch Street, London, E.C., of which business, in due course, he became a member. Burnt Ash Lane, Shooter's Hill, Crown Wood, Chiselhurst, where much of his early collecting, often with Mr. Walter Dannatt, was done, now gave place to visits to Deal, the New Forest, and other then well-known resorts of the followers of the net and pin. In course of time opportunity occurred to obtain insects from far off lands, and he gradually secured many of the larger and more conspicuous representative species of the orders Lepidoptera, Coleoptera, Orthoptera, and Hemiptera, at the same time increasing his library to embrace information on his more recent acquisitions.

In his 20th year, 1884, he joined the Entomological Society of London (now the Royal Entomological Society), and years after in 1912-14 he was elected to the Council. In 1889 he joined the Zoological Society of London, and for a time his love for living animals took up a good portion of his leisure. Especially was he attracted to snakes, lizards, and animals not generally in public favour. At one time he had a young crocodile as a pet. His visits to the gardens were frequent, and for some time he was a member of the Audit

Committee of the Society. For many years his name appeared on the List of Members of the Ray Society, and he sat on the Council at one period.

In 1892 he joined the Linnean Society, and from 1918 to 1922 served on the Council.

Not only was he an active member and regular attendant at the more important natural history societies of the metropolis, but in the activities of the local scientific bodies he early took part. Of the West Kent Scientific Society he was a member for some 45 years, acting as Hon. Secretary for most of that period. Of the South London Entomological and Natural History Society, that energetic and enthusiastic association of nature lovers from whence so many recruits are obtained for our more specialized societies, for a lengthy period he was the Hon. Secretary, which post he was induced to take by his friend and fellow collector the late Jenner Weir, the President in 1893. He retained this office until 1931, when growing general infirmity compelled him to retire. Subsequently he was elected an Hon. Member. He had, for the two years 1918-19, been president of this Society. At its popular field meetings he was almost invariably present, and usually made all the arrangements for these gatherings.

One or two collecting trips on the Continent of Europe with the late Dr. Chapman and the late J. W. Tutt were the extent of his foreign experiences. He wrote but little, confined to a few notes on his captures.

In his earlier days, and while his circumstances permitted, he was most generous to all who asked for aid in their studies. He was never married.

On the death of his father, and the transfer of the business to others, his resources were much curtailed, and as he became more infirm he gradually parted with his library and collections. His declining years were spent in a nursing home at Harrogate, until in March last he passed gently away.

HY. J. TURNER.

By the death of Dr. WILLIAM THOMAS ELLIOTT on 23 April 1938 the Linnean Society lost a member whose researches in both the plant and the animal kingdoms brought him renown both in Britain and the world at large. Born in East Anglia eighty-three years ago Elliott was from his earliest days of a studious nature—reading even on his way to and from school. He read widely on all subjects that claimed his interest, and accumulated a large and comprehensive library. During the latter part of his life he lived at Arden Grange, Tanworth-in-Arden, a half-timbered house standing in grounds screened from the road by an exceptionally fine rose-garden and a spinney of coniferous trees. Within

these grounds Elliott established colonies of *Myxomycetes* on leaf-mould and fallen logs. Families of Roman snails, some of them in their third and fourth generations, and slugs were scattered about the garden, and a small glasshouse contained a collection of Cacti. Indoors his library and collections of *Myxomycetes*, shells and dental relics never failed to arouse the admiration and interest of a visitor. Whenever the weather permitted him to do so Elliott was in his garden watching and studying these plants and animals which he had collected. The knowledge he acquired from his much loved books and the experience he gained by watching the daily life of these plants and animals gave him a fund of interest which is seldom the lot of one man. His enthusiasm was unbounded, and he was always ready and willing to help anyone whose interests lay in the fields of science in which he was himself a master.

On leaving East Anglia Elliott was apprenticed, along with Richard Winfrey (later Sir Richard Winfrey), to a firm of chemists in London, but both of them turned their attention to other professions—the former to dentistry, the latter to journalism and politics. After obtaining the L.D.S. Elliott practised in London, and later also in Birmingham and Stratford-on-Avon. He abandoned the London practice about 1912 and the Birmingham practice about 1926, but retained his connection in Stratford-on-Avon until October 1936.

It may be of interest to Fellows of this Society to know that as an apprentice dentist Elliott visited the widow of Sir James Edward Smith, who founded The Linnean Society of London in 1788. She was nearly a centenarian.

At the beginning of this century Elliott studied dentistry in America, lectured in the Dental Departments of Toronto and of Chicago University, and received the degree of D.D.S. from the University of Toronto. In Birmingham he was a member of the dental staff of Queen's College (Medical School), and later of Mason College when Queen's College became a department of the latter. He served on the staff of the Stratford Hospital for twenty-seven years, and was one of its two senior members at the time of his retirement. He was one of the first dentists in the Midland area to use cocaine as a local anaesthetic. His collection of old dental instruments include many which look more like instruments of torture than instruments to alleviate suffering, and dentures, although made with bone and containing human teeth and possibly representing a high degree of craftsmanship, which look sadly deficient in comfort.

Perhaps it is as an authority on the *Myxomycetes* that Dr. Elliott was most widely known. He received specimens for identification from most parts of the world, and he has

assembled collections of these organisms for universities and institutions in Australia, New Zealand and the United States of America. He was always ready to help any beginner by identifying his specimens, showing him how to mount them for herbaria, and indicating the critical points that should be used as taxonomic criteria. But he was also deeply interested in the living organism, and many of his observations on their activities which have been published in scientific journals resulted from the study of the colonies established in his garden.

He was a member of several scientific societies and well known in masonic circles in Birmingham, and a Past Master of the Alma Mater Lodge.

He suffered from considerable ill-health in his later years, but he did not allow this to interrupt his study of plants and animals, although it did prevent him from attending many of the meetings at which he was previously a familiar figure.

He worked with a will at anything to which he set himself, and he was a most conscientious correspondent. This was the man as the world knew him ; but to those who were permitted to visit him at home I would recall this picture :—a pleasant green lawn bounded by a splendid rock-garden and the corner of a rose garden ; a mature, half-timbered house, and a line of trees through which a view of distant fields comes pleasantly to the eye ; sitting on a chair in the shade of the trees a man of medium height reading a book or examining some specimen. When spoken to, the man's face brightens and his eyes light up with interest : he is ready to instruct, to inspect, or to argue upon almost any topic of natural history ; but to see him fully alive and radiating enthusiasm one must ask to see either the snails, the slugs, or the Myxomycetes living in this garden. Then the visitor finds the man brimming with a wealth of knowledge of the living plants and animals and anecdotes of this or that collecting excursion ; and his real vitality is apparent. Any one who has walked with him through this garden and been shown his cultures, living as they were meant to live, owes him a debt of gratitude for his recognition of the simple fact, that too often escapes us today, that plants and animals may be profitably studied in their natural surroundings.

Having lived a full and active life, Dr. William Thomas Elliott was laid to rest at Thrandestone Churchyard, Suffolk, on 27 April 1938.

CHARLES G. C. CHESTERS.

ALFRED JAMES EWART, the first occupant of a Chair of Botany in an Australasian University, was born at Liverpool on 12 February 1872, the son of Edmund William Ewart of

Scottish descent. He was educated at the Liverpool Institute and Liverpool University, where he read for the London Science Degree. After a period as demonstrator in the Botany Department at Liverpool, he was awarded an 1851 Exhibition Research Scholarship. He proceeded to Leipzig, where he worked under Pfeffer, 1894 and 1895 (Ph.D. Leipzig, 1896). In 1896-1897 he spent some months in Java working in the Buitenzorg Laboratories under Treub, applying the newer physiological methods to plants growing in the tropics. In September 1897 began an association with Mason's College, Birmingham (later the University of Birmingham), which lasted until his departure to Australia. He acted as Deputy Professor of Botany, and in 1905 was made special lecturer in Plant Physiology. He was also lecturer in Botany at the Municipal Technical School and for a time Science Master at King Edward's School in Birmingham. During this period he worked at intervals in the Department of Botany at Oxford on Protoplasmic Streaming and began the translation of Pfeffer's *Physiology of Plants*. He matriculated as a non-collegiate student at Oxford in 1898, and proceeded to the B.Sc. 1906 and D.Sc. 1910.

In 1905 the Government of Victoria decided to appoint a Government Botanist. Baron Sir Ferdinand von Mueller had died in 1896, but no successor had been appointed at the Melbourne Herbarium. The duties of Government Botanist were to be combined with those of Professor of Botany in the University of Melbourne, where, up to that time, there had only been a Chair of Biology. In 1906 Ewart took up the heavy double burden, spending half of each day at the Herbarium at South Yarra and half at the University at Carlton, some miles away across the city. This arrangement continued until 1921, when the two positions were separated and Ewart was free to devote his full time and energy to teaching and research. Conditions were still difficult for him. There were no proper Botanical Laboratories, Botany and Zoology continuing to share the single building erected for Biology. For many years this had been much too small for their joint needs. Ewart records that there were only six members of his first class in 1906. In 1929, when his Department moved to the fine new Institute of which he was justly proud, there were 220 undergraduates in the various faculties, besides staff and research workers. Unfortunately Ewart did not long remain in good health to enjoy the improved working conditions. He developed heart trouble and was compelled to rest for long periods. He had been unable to carry out his duties during the greater part of 1937, but it was hoped that he would be able to return for the third (Michaelmas) term, at the end of which he was due to retire. It was not to be.

He died suddenly at his home on 12 September 1937, in his 66th year.

Ewart was a man of strong physique, who delighted in the opportunities for open-air life which Australia afforded. He had a cottage and small estate at Chum Creek, near Healsville, where many of his vacations were spent in hard physical work clearing and cultivating his land. In his youth he had played football, and, after settling in Australia, he became interested in the Australian game, which he held was much superior to the English from the spectator's point of view. A man of simple tastes, he had essentially a kindly nature and a fondness of children. He had, unfortunately a hot temper which led him at times into discussions and polemics, and prevented him from taking that share in the development of the Botanical Services in Australia which his scientific standing would have warranted. But Australian botanists, and particularly those of Victoria, will remember the work of Ewart as a systematic botanist. This is the more remarkable since he trained as a physiologist.

Ewart's work may be divided into two periods. First, that of the laboratory physiologist before he went to Australia, and, secondly, that of the herbarium worker with a strong 'economic bias' after he had settled at Melbourne. This division can hardly have been one of choice, but for many years he had neither the time nor the facilities for much physiological work. During his time in Leipzig he investigated the conditions which inhibit Assimilation, making use of the bacterial method of demonstrating assimilatory activity. These researches were published at length in the *Journal of this Society* (vol. xxxi, 1896). In Java he studied the effects of tropical insolation on assimilation and also the response to contact stimuli by climbing organs (*Ann. Jard. Bot. Buitenzorg*, xv, 1898).

During the next ten years Ewart published on such a considerable range of physiological subjects as Problems of Assimilation; The Function of Chloroplasts; Protoplasmic Streaming (*Oxford*, 1903); and the Ascent of Water in Trees (*Phil. Trans. Roy. Soc.*, 1905 and 1908). He also found time to translate Pfeffer's *Physiology of Plants* (*Oxford University Press*, 1899-1906) and to write a text-book of Matriculation Botany.

When Ewart reached Australia in 1906 he found that the routine duties of a Government Botanist and Keeper of a large Herbarium necessitated activity in quite another field. Nevertheless, one sees in his papers on the Longevity of Seeds (*Proc. Roy. Soc. Vict.* xxi, 1908), and on Transpiration under Australian Conditions (*Ann. Bot.* xxiv, 1910) how he tried for a time to continue physiological work. His later papers

on Chlorophyll and Assimilation (Proc. Roy. Soc. Vict. 1918-1920) are less important. In pure taxonomic work he published a series of thirty-six Contributions to the Flora of Australia; compiled a Flora of the Northern Territory (1918), and, finally, in 1930 was able to complete his 'Flora of Victoria', a work of over 1,000 pages, with some 400 illustrations. This had long been an ambition. There was no Flora in existence except a Key published by von Mueller in 1888. Any critical work required reference to the 'Flora Australiensis', which not only covers the whole continent, but also needs revision and extension in the light of later work.

His consulting and advisory work for the Government brought Ewart into frequent contact with problems of weed introductions, poisonous plants, timber conservation, and forestry generally. As early as 1909 he published a useful semi-popular work on 'The Weeds, Poisonous Plants and Naturalised Aliens of Victoria'. In 1924 he spent some months in Central Australia inquiring into stock poisoning on the overland stock route. Again in 1927 he visited the Kimberley district of Western Australia investigating the obscure disease of horses known as 'Walk About'. These he believed to be due to saponin poisoning. Ewart thoroughly enjoyed these visits to the distant parts of Australia. The writer remembers spending several days with him at Alice Springs in 1924, and his delight in the new scenes and experiences. But the conditions, especially in the Kimberley district in 1927, must have been a severe tax upon a man of his age.

The need for trained forestry workers led him to take much interest in forestry education. In 1925 he published 'A Handbook of Forest Trees for Victorian Foresters'. At the time of his death he was Chairman of the Forestry Examination Board.

Ewart was President of Section M (Botany) of the Australian and New Zealand Association at the Perth Meeting in 1926. He became a Fellow of the Linnean Society in 1898. In 1922 he was elected F.R.S.

T. G. B. OSBORN.

SIR CECIL HANBURY.—The untimely and unexpected death of Sir Cecil Hanbury on 10 June, 1937, is a great loss both to Botany and to Horticulture. He ably followed his distinguished father, Sir Thomas Hanbury, in maintaining and developing the beautiful gardens at La Mortola, Ventimiglia, Italy, and retaining their botanical character, which renders them of so much value to botanists generally. Just before his death he and Lady Hanbury had completed the manuscript of a new edition of the 'List of Plants in cultivation at La Mortola'. This was carefully checked at Kew, Sir Cecil having brought

it down for the purpose a few weeks before his death, and has now been published.

The living collections at La Mortola are especially rich in representatives of the floras of South Africa, and South and Central America, and Sir Cecil was always anxious to make interesting additions to his collections. He also maintained and added to the botanical museum, herbarium, and library established by Sir Thomas.

He was a Governor of the Imperial College of Tropical Agriculture, and had been member of Parliament for North Dorset since 1924.

A. W. HILL.

FREDERICK JANSON HANBURY died on Tuesday, 1 March 1938, at his home, Brockhurst, East Grinstead, having attained the advanced age of 86 years. Mr. Hanbury, the eldest son of Cornelius Hanbury, was born at Stoke Newington, London, N., on 27 May 1851, and was educated at the Friends' School, Grove House, Tottenham. Being born into a family of pharmacists, he was apprenticed in 1868 with Mr. Henry Deane of Clapham to learn the art of pharmacy; this was followed in 1871 and 1872 by a period of study at the College of the Pharmaceutical Society of Great Britain in Bloomsbury Square, London, leading to the examination for the qualification of Pharmaceutical Chemist, which he successfully obtained in December 1872. He then entered the old family business carried on at Plough Court, where he was associated with his father and his cousin Daniel Hanbury, joint author with Plücker of 'Pharmacographia'. The study of botany early attracted the attention of F. J. Hanbury, who constantly went botanizing on Clapham and Wandsworth Commons during his apprenticeship, using Bentham's 'Botany' for the identification of the plants which he collected and made into a herbarium to be entered for the competition held annually by the Pharmaceutical Society; for this collection he was awarded a silver medal. Botany continued to be his favourite subject of study and brought him the friendship of Dr. Henry Trimen, who encouraged Hanbury to compile a 'Flora of Kent', which was eventually published in 1899, after a long and careful investigation extending over 40 years; in the preparation of this Flora he was assisted by his life-long friend and joint author, the late Rev. E. S. Marshall, then Vicar of Milford, Surrey. In succession to Dr. Boswell Syme he became editor of the 'London Catalogue of British Plants'. A third valuable contribution to scientific botany was made by a critical study of the genus *Hieracium*, and he described many new species and varieties of this genus in papers published at intervals over a period of several years. Mr. Hanbury further showed his interest in systematic botany by purchasing

Dr. Syme's extensive herbarium and presenting it to the Botanical Department of the British Museum (Natural History), which was thus enriched by the addition of about 70,000 specimens.

A keen interest in horticulture, more especially in the cultivation of rock-garden plants and of orchids was another aspect of Hanbury's botanical work. His rock garden at East Grinstead is famous for the many rare plants grown on a rockery carefully constructed from the natural sandstone subsoil. For his orchids he received many notable awards, and in 1924 he was awarded the Victoria Medal of Honour of the Royal Horticultural Society, upon the Council of which he served for several years. In 1926, the Royal Academy of Sciences of Sweden awarded him the Elder Linnean Medal in gold.

Throughout a period of 70 years Mr. Hanbury took an active share in the management of the business of Messrs. Allen and Hanburys Ltd. During the early years of his connexion with the business, he also acted for the years 1877 and 1878 as a member of the Board of Examiners of the Pharmaceutical Society of Great Britain. The business, originally at the Plough Court Pharmacy in the City of London, underwent great expansion and many changes during Hanbury's lifetime, and from 1916 to 1937 he was chairman of the board of directors.

Outside his scientific and business activities Mr. Hanbury took an active part in Church affairs, and was representative of the London Diocesan Council and also the Chichester Diocesan Council at the National Assembly of the Church of England; he was churchwarden of St. Mary's, East Grinstead, and also of St. Edmund the King, Lombard Street.

He married, in 1874, Mary Jane Scarborough, daughter of Robert King of Upper Clapton, and had three sons and three daughters. Two of his sons, Mr. Reginald Janson Hanbury and Mr. Frederick Capel Hanbury, are at present directors of Messrs. Allen and Hanburys Ltd.

T. E. WALLIS.

RICHARD VON HERTWIG (he acquired the distinction of *von* too late in life for it to appear on his more important writings) was born on 23 September 1850 in Friedberg (Hesse), but spent most of his childhood at Mühlhausen (Thuringia) where his father was a well-to-do manufacturer. In his youth Richard, with his equally distinguished brother Oskar (subsequently professor at Berlin), studied science and medicine first at Jena (1868) and afterwards at Zürich and Bonn. He took his medical degree at the latter university (1873), and graduated *Dr. phil.* in zoology at Jena two years later. Here he became extraordinary professor in 1878,

and in 1881 full Professor of Zoology at Königsberg. In 1883 he was appointed to a similar chair at Bonn, but soon relinquished it to take up the professorship of zoology at Munich (1885). This post he held with distinction for forty years, retiring as *professor emeritus* in 1925. His school and his influence are therefore now inseparably associated with the Bavarian university.

Of his own teachers Hertwig himself spoke eloquently at the celebration of his sixtieth birthday (1910), when an imposing *Festschrift* was presented to him by his many friends and pupils. 'With love and gratitude', he said, 'I recall all those men who had a lasting influence upon my scientific development in early days. In the front rank stands Ernst Haeckel . . . And I remember also, with thankfulness, my two other great teachers, Carl Gegenbaur and Max Schultze, with whom it was likewise my privilege to be on terms of intimate friendship. But above all I think of my brother. We sat together on the same form in school, studied together and took our examinations together, and till thirty years of age planned and published together much of our research. My brother is a year and a half my senior, and was, from an early age, of a contemplative nature, envisaging all things with unusual earnestness. It is therefore understandable that he exercised a quite dominating and directive influence upon me, the junior and more compliant partner.'

The early work of the two brothers is now famous. It includes their classical investigations of the nervous system in Coelenterata, and studies of the fertilization and cleavage of the sea-urchin egg—the latter a work of capital importance in the history of cytology and genetics. Later, Richard turned his attention to many other subjects—particularly, in latter years, to the study of sex-determination and the general biology of sex. But throughout his life he devoted his abundant energy largely to the study of the Protozoa, and it is by his researches on these organisms, probably, that his name will be most enduringly preserved. It is noteworthy that his inaugural dissertation for his doctor's degree (published in 1875) dealt with a marine Acinetarian.

But Richard Hertwig was not a protozoologist in the narrow sense: he lived at a time when it was still possible to 'specialize' in many subjects, and protozoology was only one of his many interests. Nevertheless, he contributed much to our knowledge of the Protozoa, and for many years his Institute at Munich was a centre of great protozoological activity. Not only did he perform researches himself which can now be fairly described as 'classical', but he also inspired and supervised a vast amount of original work which was carried out by his pupils and colleagues.

Hertwig's own contributions to protozoology—apart from the work of his pupils—are contained in a long series of monographs and papers covering a wide field and extending over more than half a century. Many of his researches, however, were incorporated in general works—discussions of evolution, sex-determination, and other broad biological problems—so that the protozoological elements are not always readily separable. But certain of his publications were of outstanding protozoological importance, and have left a permanent impression on the science. Among these must be mentioned the following :

(1) His early studies of the free-living Rhizopods, of which the most notable is the monograph (with E. Lesser) published in 1874. Here are to be found many new and accurate observations on the morphology and physiology of these organisms.

(2) The monograph on the Radiolaria (1879), which helped to found our present knowledge of these forms and established their 'unicellular' constitution.

(3) His studies of the conjugation of the 'Infusoria' (1889), which is truly a classic. These researches added much to the information elicited by Maupas and other early workers, and showed Hertwig at his best. He here recorded at least two fundamentally novel points, in addition to confirming and extending many important observations made by others. He showed that conjugation in *Paramecium* is not—as was then generally believed—a kind of 'rejuvenation': and he anticipated the discovery of 'endomixis' (by Woodruff and Erdmann, 1914). The first point was demonstrated by an ingenious experiment which has since been fruitfully repeated and extended. (He forcibly separated individual organisms which had paired for conjugation, and cultivated them further: and he thereby showed that they were not 'senile' or in any way debilitated individuals at the end of their life-cycle, but fully vigorous and 'vital' and capable of further asexual reproduction indefinitely.)

(4) The monograph on *Actinosphaerium* (1898) is another undoubted classic, and would alone establish Hertwig's reputation as a first-class protozoologist. This memoir contains the first full and accurate account of the life-history of any heliozoon, and elucidates the remarkable sexual phenomena and nuclear changes characteristic of the genus. The 'autogamy', which Hertwig carefully described, led to a vast amount of speculation and discussion—most of it now appearing fallacious and unjustifiable—but the facts which he established are still unshaken. His later work on the 'physiological degeneration' of the same organism (1904) was equally productive of speculative results, but has now fallen into oblivion.

(5) The memoir on *Arcella* (1899) contained an abundance of facts, and gave further cause for speculation. It also contained the seeds of the 'chromidial theory', which once achieved great popularity and was elaborated in

(6) 'The Protozoa and the Cell-Theory' (1902). This once famous paper was written by Hertwig as an introduction to vol. I of the *Archiv für Protistenkunde* (founded by Schaudinn), and exercised a profound influence upon the development of protistology (and general cytology) for over a decade. He here first enunciated his conception of 'chromidia', which gave rise to an enormous amount of speculation and research. Hertwig's ideas here again proved extremely fertile, but they produced—in this instance—little of permanent value.

His protozoological and other investigations finally led Hertwig to propound a 'theory' of his own to account for vital phenomena in general. This was his once well-known *Kernplasmarelationstheorie*, or theory of the 'karyoplasmic ratio', which sought to explain all the activities of the cell—and consequently of the organism as a whole—in terms of equilibrium between nucleus and cytoplasm. The best exposition of this concept is to be found in the essay 'On new problems of cytology' which he contributed to the first volume of Goldschmidt's *Archiv für Zellforschung* (1908). This 'theory' is in many ways characteristic of Hertwig. Brought up 'after the most straitest sect' a morphologist, he yet understood to the full the importance of physiology and experimental methods. And consequently, though all his work was dominated by what he called 'the two great biological theories of the nineteenth century' (the theory of evolution and the cell-theory), it is still sufficiently modern in outlook to be read and appreciated by present-day students.

Hertwig was a man who had countless friends and few enemies. His pupils too were innumerable, and they all regarded him with respect and affection: at least, I have never met one who did not. We all, I think, consider it a privilege to have worked with this warm-hearted and industrious little man in the *Alte Akademie* at Munich; for he was father—perhaps I should say grandfather—to an immense and devoted zoological family, which had a cosmopolitan distribution and is still alive and active at the present day. He himself belonged to many scientific societies at home and abroad (he was elected a Foreign Member of the Linnean Society in 1911), and held the highest academic offices—including that of *Rector Magnificus* of his own university: yet he was always ready and able to discuss any big biological problem or small technical detail with the least of his first-year students or the greatest expert. And his influence

radiated, moreover, far beyond his personal sphere through his *Text-book of Zoology*, which has instructed an untold number of students in the rudiments of their science and art. (The first edition appeared in 1890, and it is now in its fifteenth.) At the festivities organized in 1925 to honour his 'century'—100 university semesters faithfully discharged—an address was presented to him bearing the signatures of no less than 208 of his actual pupils then living (representing seventeen different nations).

Historically it remains to add, as a sad but inevitable *ultima linea*, that Hertwig died on 3 October 1937. He died at his country home in the Isar Valley (near Munich) where he had spent the remaining years of his life after his retirement. Ten days previously he had celebrated his eighty-seventh birthday, apparently in full bodily and mental vigour; so he passed away, happily after only one day's illness, appropriately near the spot where he had formerly collected many of his Rhizopods and Ciliates and his beloved *Actinosphaerium*.

CLIFFORD DOBELL.

CHARLES HENRY NICHOLLS was born on 30 December 1866, at Hawkhurst Court, Kirdford, Sussex. He died at Watlington Cottage Hospital, after six months' severe illness, on 15 January 1938, aged 71.

Nicholls was educated at Winchester School and New College, Oxford. After taking the degree of B.A. in Natural Science in 1890, he continued his botanical studies in the Herbarium of the Royal Botanic Gardens, Kew, and subsequently did research work in the Herbaria of the Royal Botanic Gardens at Cinchona, Jamaica (where he did special experimental work on sisal hemp, the results of which were recorded in the *Journal of the Botanic Garden*), at Peradeniya, Ceylon, and at Edinburgh. In May 1893 he was elected a Fellow of the Linnean Society.

He specialized in economic botany, and had a wide knowledge of the subject, on the purely botanical, as well as on the agricultural, side.

From 1894 to 1895 he held an appointment at the Board of Agriculture, but resigned in order to exchange administrative work for scientific research. He afterwards worked for the English Agricultural Organization Society, the Irish Agricultural Organization Society, and helped in the compilation of the *Geographical Index of the Encyclopaedia Britannica*.

From 1903 to 1909 he was on the staff of the Imperial Institute, and when he left the service his post was that of Technical Superintendent. During his term of office he had been responsible for a number of articles dealing with the

cultivation, preparation, and utilization of various tropical crops published in the 'Bulletin of the Imperial Institute'. For some time he took charge of a section of the Colonial Collections in the Exhibition Galleries and paid particular attention to the arrangement and description of the collections illustrating the natural resources and economic products of Australia, in which connection he took part in the production of several reports connected with the utilization of Australian commercial products.

During the War he worked at Wye Agricultural College at experimental work on food preservation and held a post at Abbotsholme School, Derbyshire.

Outside his purely scientific work his chief hobby lay in the planting of trees, doing this especially at Withurst in Sussex, where his plantings now form a remarkable feature of the countryside. He planted trees there every year, especially Scot's pine, Larch, Ash, Austrian pine, and Douglas fir, and always had a nursery of trees ready.

A beautiful woodland industry (hoop shaving) was carried on in the copse and plantations every few years when the undergrowth was in a suitable condition.

A. W. ANDREWS.

ROGER CROMPTON NOTCUTT, the son of Stephen Abbott Notcutt, solicitor and Town Clerk of Ipswich, was born in 1869 and died suddenly on 30 January 1938.

Few men enjoy the public and private esteem in which he was held. A living contradiction of the adage that a man is without honour in his own country, no man was more respected in his area of Suffolk than he. And no wonder. The word 'trouble' did not occur in his vocabulary. His immense energy was freely spent on the welfare of Woodbridge. No public body from the Urban District Council, of which he was chairman, to a small local committee was complete without him. Always modest and unassuming, he held his influence by sweet reasonableness and an unquenchable enthusiasm for all that he considered good. But he went further than that. Not satisfied that his work on the Suffolk Preservation Committee and on the Breckland Committee of the Council for the Preservation of Rural England fully represented what he took to be his part in the conservation of our country, he purchased out of his own pocket Kyson Hill, a famous beauty spot near Woodbridge, and presented it to the National Trust in 1934.

His horticultural interests were mainly directed towards trees and shrubs, and on their garden value and cultivation he had an international reputation. His writings were informed by a profound knowledge, and his counsels, more

than mere expressions of faith, were carried into his own practice and no plant bearing the name of his nursery required further guarantee of authenticity and excellence.

A keen student of old Herbals, Floras, and other botanical books, his large collection of such works shared the shelves of his library with volumes on the History of Suffolk, another of his absorbing interests.

Notecutt lived a full life and lived it well. A chance remark he once made to the writer indicated his enjoyment of it. 'I believe', said he, 'that boredom is just an affectation'.

F. STOKER.

FRANK ARMITAGE POTTS, University Lecturer in Zoology and Fellow of Trinity Hall, Cambridge, died after a brief illness on 15 September 1937. He was the younger son of a well-known Wesleyan Methodist minister, from whom he inherited a love of learning and a degree of personal modesty by no means common. At an early age he showed an interest in natural history, and, when ten years old, he could not infrequently be found in the local museum at lunch-time fully equipped for the nourishment of both mind and body. Throughout his life he retained many of the characteristics of what must have been a happy and attractive childhood.

After four years at Kingswood School, Bath, Potts went into residence in 1901 at Trinity Hall, Cambridge: of that Society he remained a member until his death. In 1905, after a brilliant career as an undergraduate, he obtained the remarkable distinction of being placed in the first class in both Geology and Zoology in the second part of the Natural Sciences Tripos—a feat which has never been, nor is likely to be, repeated. In 1908 he was elected a Fellow of his College. As a graduate, Potts was essentially a zoologist: but he retained his interest in geology, and there were few things which he enjoyed more than his association with his fellow-members of the Sedgwick Club and his excursions with them into the field. As a zoologist, he was one of a distinguished group of young men resident in Cambridge from 1906-8: and he quickly established himself as an authority on the Polychaeta by his description of the collections brought home from the Indian Ocean by Prof. J. Stanley Gardiner. These descriptions were published in the Transactions of the Society in 1909 and 1910. Meanwhile, Potts had worked in Naples with Geoffrey Smith (who was killed on the Somme in 1916). This association aroused an interest in the Rhizocephalia and led to the publication of two important papers, one on *Mycetomorpha*, a new genus found off Vancouver Island in 1911, the other on *Thompsonia* found on the Great Barrier Reef in 1913. In 1913 he published, in the Quarterly Journal of Microscopical

Science', his well-known paper on the 'Stolon Formation in certain Species of *Trypanosyllis*' and began his work on the life-history of the free-living Nematodes. All Potts' papers showed a mastery of the problem involved and were characterized by clarity and brevity of exposition. During the years 1908-1914 he not only visited the Pacific and other areas of zoological interest, but he also published work which was truly remarkable both in quantity and in quality.

At the outbreak of war in 1914, Potts immediately applied for a commission in an infantry battalion. He joined the Border Regiment and served in France for the whole duration of the war. After a period of regimental duty, he was transferred to the gas services; and at the armistice he was Commandant of one of the most successful Gas Schools in France. Full of humour and full of courage he infected all his associates with the spirit of light-hearted determination which was so characteristic of himself. In later years he seldom spoke of the War, partly because he felt too strongly its tragedies and its disastrous effects on principles in which he himself never ceased to believe.

On his return to Cambridge in 1919, Potts devoted much of his time to University and College affairs. For ten years he was Assistant Tutor at Trinity Hall, and he won the affection and respect of the undergraduates of his College. He served on many committees and he did much valuable work as a Syndic of the University Press. As a formal teacher he was conscientious and efficient; but it was as an informal and friendly director of studies that he felt most at home. Few teachers have won the friendship of their pupils in quite the same way, and as a guide and friend of youth he had few equals. He was not particularly interested in administrative problems and, at times, his disregard of detail might be embarrassing, but, at moments of crisis, he seldom, if ever, failed.

In many ways Potts was the best type of Cambridge don, keenly interested in each of his pupils and widely known throughout the University. Few residents did not enjoy his acquaintance, and his cheerful, almost boyish, personality was an attractive feature of University life. As a guest he was always welcome, and to lunch or dine with him in Trinity Hall was an invitation as eagerly accepted as it was readily bestowed. To his contemporaries, to undergraduates, and to zoologists in general, Potts gave unselfish and loyal friendship.

His later years were less fruitful than his earlier in scientific work, as the impulse for creative research was never quite regained after the War. More and more he gave himself to the encouragement of his friends, in whose achievements he took a sincere delight. In other ways he found these years a source



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ALFRED BARTON RENDLE

Photo by The Sport and General Press Agency Ltd.

of happiness. In 1926 he married Lilian Gertrude, the sister of his friend T. C. Nicholas, and had a son. Most of the time he could spare from Cambridge was spent at West Runton, in Norfolk, where he had built a delightful cottage and where it was hoped he would spend many happy years in later life. This was denied to him. His untimely death at the age of 55 is a loss not only to the subject which was near to his heart, but to many friends to whose hearts he was always very near.

J. GRAY.

ALFRED BARTON RENDLE (1865-1938) was born in London on January 19th, 1865, the eldest child and only son of John Samuel and Jane Wilson Rendle. After attending a school at Lewisham he went to St. Olave's Grammar School, Southwark, and from there succeeded in obtaining a scholarship to St. John's College, Cambridge. Before going up to Cambridge he seems to have received more instruction in naming plants than was usual and he often mentioned how, when at Cambridge, finding an old volume of Mrs. Hooker's translation of *Le Maout and Decaisne* in the greenhouse at the Botanic Garden, he used it to identify the plants in flower. It was an interesting period in Cambridge Botany, for S. H. Vines had been introducing new ideas into its teaching. Nothing perhaps would have pleased Rendle better, after taking his Part II in Botany, than to have joined the band of students attached to Vines. Just at that period, however, Vines left Cambridge to become Sherardian Professor of Botany at Oxford. Rendle wrote three small papers on his botanical researches at Cambridge:—on the development of aleurone grains in the lupin, the occurrence of starch in the onion, and the 'vesicular' vessels of the onion—a preliminary account of the last being published in collaboration with Vines.

While Rendle was on the look-out for a job, a vacancy occurred in the Department of Botany, British Museum, owing to H. N. Ridley's appointment as Director of Gardens and Forests, Singapore, and Rendle was appointed Assistant (1888), his special groups being *Apetalæ*, *Monocotyledons*, and *Gymnosperms*. He applied himself conscientiously to his studies, paying particular attention to *Monocotyledons*, which remained his chief interest throughout his official career.

Immediately on taking up his duties, he sought election to the Linnean Society. The then Keeper of Botany, W. Carruthers, was President at that time, and Rendle often referred with evident pleasure to the fact that he had been admitted to the Society by his chief. From the beginning he took an active part in the meetings, and his earliest important paper, 'Revision of the Genus *Nipadiates* Bowerb.', was published

in the Society's Journal (xxx, pp. 143-54; 1895), and his 'A Systematic Revision of the Genus *Najas*', which was his thesis for his London D.Sc., in the Transactions (ser. 2, v, pp. 379-444; 1899). He served on the Council for four periods (1899-01, 1904-8, 1909-12, and 1915-16) and in 1916 he succeeded O. Stapf as Botanical Secretary, continuing in this office until he was elected President in 1923, a position he held for four years. He was thus an officer of the Society during the last half of the war and for nine years afterwards—perhaps the most difficult period in its history. His service to the Society was whole-hearted, and though perhaps he did not initiate some of the moves which were made to enable the Society to continue its work efficiently he was ever ready to discuss any suggestion from every point of view, and to help forward with considerable enthusiasm anything which he felt was beneficial to the Society or to the biological sciences. After relinquishing the Presidency, his interest in the Society did not diminish and he attended the meetings regularly, occasionally contributing papers and frequently taking part in the discussions. During the last sixteen years I discussed freely with him every aspect of Linnean affairs, and I can remember no instance, no matter what the circumstances, when the welfare of the Society was not for him the paramount consideration. It gave him great pleasure, after his period of office, to be re-elected to represent the Society on various bodies, as for example on the Lawes Trust Committee of Rothamsted, on which he did valuable work for many years.

Rendle always took an interest in academic botany. He had done a small amount of demonstrating at Cambridge and in 1894 he was appointed lecturer in botany at Birkbeck Institute. Doubtless the work appealed to him greatly, but he probably would not have undertaken such heavy evening duties if it had not been that he welcomed the additional salary. Many of his old students speak with enthusiasm of the help he gave them in their struggle to gain a University degree solely by evening work. It was a period of transition for Birkbeck, for during the twelve years he was associated with it there was continuous effort to obtain its recognition as a constituent college of the University. By a strange coincidence the change occurred in 1906, the year he was appointed Keeper of Botany in succession to George Murray, and he resigned. He continued to serve on the Botany Board of the London University for several years and examined in the Cambridge Local Examinations long after his retirement from the Museum.

Another aspect of his interest in teaching was the writing of his 'Classification of Flowering Plants'. He had given a University Course of lectures at the Chelsea Physic Garden

in 1902, and published the first volume of his text-book in 1904. This dealt with Monocotyledons and Gymnosperms. The second volume did not appear until 1924. It treated those flowering plants with which, for the most part, he was least familiar, but the delay was not due to this but to the many ways in which his unofficial time was occupied; as it was so long in preparation he twice re-wrote it. A second edition of the first volume appeared in 1930. The work is carefully done and has a deservedly high reputation among teachers of systematic botany as thoroughly sound, though perhaps to many students it is not very inspiring. I know this was my own idea about the first volume when I was an undergraduate, but in those days we were rather too much attracted by hypothetical phylogenetic trees. Rendle had his own ideas on the relations between many families, but did not regard detailed speculations as worth while; he always held that certainty of identification is more important than guesses at affinity, particularly by those with little knowledge of generic and specific differences. In his introduction to Vol. II he makes a characteristic statement: 'The following arrangement does not claim to be strictly phylogenetic. Various attempts have been made to construct a phylogenetic system of Angiosperms, but the results are not convincing, bear no suggestion of permanence, and bristle with difficulties for the student.' He himself favoured Engler's system and arranged the general exhibit in the Museum Botanical Gallery by it. On the other hand, he used Bentham and Hooker's system for the arrangement of the *British Flowering Plants*.

He was a great believer in the educational value of systematic botany, even for children: in a letter to the '*New Phytologist*' in 1902 advocating his point of view he wrote: 'Without deprecating other methods, I think, Sir, I have illustrated one which is not over-burdened with technical terms, requires no apparatus, and has the great advantage of systematising the facts which are observed.' He was interested in the British Flora, but had not a critical knowledge of the plants. He edited the last edition of Bentham and Hooker's '*Handbook of the British Flora*', in 1924, but made no real mark on the work. His chief claim to mention in this connexion is the valuable efforts he made—both educational and legal—to obtain protection for our native flora. Indeed, the first meeting I attended at which he took the Chair was in the Society's Rooms before the War when there was a proposal to approach Parliament to have a bill passed for that purpose: and the last Presidential Address he gave was to the delegates of the Corresponding Societies at the British Association Meeting at Blackpool in 1936 on '*The preservation of native floras*'.

Another major activity was that of botanical nomenclature. The subject was much to the fore practically throughout his career. Alphonse de Candolle had put forward his 'Les Lois de la Nomenclature Botanique' at a Horticultural and Botanical Congress at Paris in 1867, and these were accepted after being reported on by a committee of eight at the last sitting. In 1891 O. Kuntze startled the botanical world by his 'Revisio Plantarum Genera', in which the names of 1074 genera and about 30,000 species were changed by the not unusual method of interpreting a rule—here that of priority—in his own way. At a Congress at Geneva the following year P. F. A. Ascherson criticized Kuntze and proposed that 1753 should be the starting-point for botanical nomenclature, and also that certain names should be conserved. A committee of thirty were appointed to go into the whole question—the first real move to modify the Candollean rules. The present series of International Botanical Congresses began with the one held at Paris in 1900; here nomenclature was discussed and a bureau formed which was to ask societies and institutions to nominate competent members: J. Briquet was appointed to compile the dossier of replies and from it to draw up a 'Texte Synoptique' for consideration at the next Congress to be held at Vienna in 1905. This Rendle attended as delegate both of the Linnean Society and the British Museum. He took an active part in the discussions, and, unlike his practice in later years, carried on informal talks far into the night—he once told me that he had tired certain recalcitrant systematists into agreement. In a speech at the official banquet Briquet described him as '*Rendlius insularis*, species anglica politate et benignitate inter omnes plantas optimes hujus regionis praestans'. A revised code of rules was drawn up, and he was appointed one of four members of an editorial committee, the others being J. Briquet (editor-in-chief), H. Harms, and L. Mangin; Rendle was responsible for the English version of the rules. He continued to serve on this committee until the publication of the revised set of rules resulting from the deliberations at the Cambridge Congress in 1930; Briquet died while the work was in progress and Rendle assumed the position of responsible editor.

Rendle took a very active part in the preliminary arrangements made for the International Botanical Congress planned to be held in London in 1915 and began the arrangements for the Congress in 1930 which it was originally intended to hold in London, but eventually was held at Cambridge. Unfortunately he was ill at the time of the preliminary meeting which he had called. He acted as Treasurer to the Congress, an office he also filled for the Imperial Botanical Conferences held in London in 1924 and 1935. He thoroughly

enjoyed an International Congress and attended not only those of Botany, but also of Horticulture. He was a regular attender at British Association meetings and was President of Section K (Botany) at Newcastle in 1916.

As is usual the period before his accession to an administrative position was the most productive in contributions to botany in the generally accepted sense, though it would be foolish to suggest that it was not in his later years that he did most to further botanical science. He contributed the section on Monocotyledons and Gymnosperms to the 'Catalogue of Welwitsch's African Plants' (1899) and wrote the account of Naiadaceae for Engler's 'Pflanzenreich' (1901), that of Gramineae in Forbes and Hemsley's 'Index Florae Sinensis' (1903), and the Convolvulaceae in the 'Flora of Tropical Africa' (1906). He helped Sir John Lubbock with his volumes on 'Seedlings' (1892) and saw the work through the press. After he became Keeper of Botany in 1906 his writings were mostly concerned with the naming of collections which came to the Museum: amongst the most important were those of R. H. Compton (New Caledonia), L. S. Gibbs (Arfak Mts. &c.), H. O. Forbes (New Guinea), B. Kloss (Annam), P. Talbot (Nigeria). He acted as Botanical Editor for the eleventh edition of the 'Encyclopaedia Britannica' (1910-11). Possibly his botanical reputation will rest mainly on the 'Flora of Jamaica' which he started in collaboration with W. Fawcett in 1910, and of which five volumes have appeared. Fawcett had been an Assistant in the Department of Botany from 1880-86 (having succeeded H. Trimen) and then became Director of the Botanic Gardens and Plantations at Jamaica. He kept in touch with the Department and received considerable help from Randle in the naming of Orchids, and, agreeing to collaborate in writing a monograph on orchids, they published an account of the genus *Lepanthes* in 1904. When he retired from Jamaica in 1908 he worked regularly in the Department, and having in mind the writing of a Flora interested Randle in the scheme and the monograph on orchids was published as the first volume (1910). The spade-work was done by Fawcett, but it was a collaboration in the truest sense of the word: it is certain that otherwise there would have been no publication. The work on the Jamaican flora also provided material for several short papers in the 'Journal of Botany'. This periodical has always been closely associated with the Department of Botany. Founded in 1863 by B. Seemann it was edited by him until 1872 when H. Trimen took it over until 1879: then James Britten became editor and owner of the Journal until his death in 1924 when he bequeathed it to Randle. The finances of the Journal had frequently been commented on by Britten, and

Rendle shied at shouldering this responsibility. He, however, made an arrangement with Messrs. Taylor and Francis, who became the owners with Rendle as editor. He had long been a frequent contributor to its pages, and had seen numbers through the press when Britten was away. Previously the notes by the editor were always liable to cause a little uneasiness, and the Keeper of Botany was often appealed to. He was anxious about the future of the Journal and was very gratified when it finally came into his own hands.

Britten also bequeathed him the 'Biographical Index of British Botanists', a valuable work the second edition of which G. S. Boulger (died 1922) and Britten had been engaged on for many years. This edition, which had been financed by Britten, was published by Rendle in 1931.

Rendle took an active part in the work of the Royal Horticultural Society. When I first went to the Museum he used to attend the Scientific Committee meetings regularly, and later, when G. Henslow retired, he became Honorary Professor of Botany to the Society. He was also a member of various committees, but took most interest in the Wisley Gardens, being a member both of the gardens committee and of the Wisley Scientific Committee. He played a leading part in the conduct of the Society's examinations and gave occasional lectures. For his services he was awarded the Victoria Medal of Honour in 1917 and the Veitch Memorial Medal in 1929.

After his retirement from the service of the Trustees of the British Museum in 1930 he continued to work in the Department of Botany two or three times a week. He was mainly engaged in editing the 'Journal of Botany' and in working at the 'Flora of Jamaica', but his interest was always likely to be diverted by some discovery in bibliography or by some point in taxonomy. He was full of schemes to the end and frequently mentioned the hope he had of writing up the Sloane Herbarium—'when the Flora is finished, if you have no objection',—but I always felt that the enormous task was never likely to be undertaken by him. It is much to be regretted that the second volume (Monocotyledons) of the 'Flora of Jamaica' was left to the end, simply because he believed that it would present few difficulties to him.

Rendle was always keen on travel, and his main interest was in seeing a new flora. He visited Australia (1914), Canada (1925), U.S.A. (1926), South Africa (1929), and Bermuda and Jamaica (1933), most of them with the British Association: he brought back collections from all these trips, losing no opportunity, on the two on which I accompanied him at least, in obtaining botanical specimens. He was at his best on these occasions and also entered into the spirit of

life on board ship with great enthusiasm and had not inconsiderable skill at deck-games.

For the last few years he had suffered from an internal complaint, and during the summer of 1937 was troubled with duodenal ulcers. He, however, looked forward with enthusiasm to accompanying the British Association delegation to India at the end of the year. On the voyage he unfortunately caught a chill which wakened up his old complaint; he went into hospital at Bombay, hoping to be able to rejoin the party in a short time. He, however, was forced to return to England and died on January 11th, three days after he arrived home.

Many Societies both at home and abroad honoured him. He was elected Fellow of the Royal Society in 1909. He was also Associate Member of the Société Royale de Botanique de Belgique, Honorary Member of the Botanical Society of Japan and of the American Academy of Arts and Sciences, and Honorary Fellow of the Botanical Society of Edinburgh.

His quiet demeanour and his conscientious carrying out of anything he undertook, together with his keenness in all botanical matters, were much appreciated by a large circle.

He was twice married, his second wife dying a short time before his retirement. He was justifiably proud of his family of seven children.

The portrait (Plate 6) which accompanies this note was taken just before he left England. J. RAMSBOTTOM.

CHARLES GILBERT ROGERS (1864-1937) was the second surviving son of Captain Henry Rogers, R.N., of Hartley, Plymouth, and Jane Enys, both of old Cornish families. He was educated at Plymouth College and Sutton Vallence School, and entered the Indian Forest Service in 1888, passing out first from Coopers Hill Engineering College, of which he became a Fellow. He had been a prominent member of the Rugby football team of the College, and he played also for the county of Surrey.

Arriving in India he passed his language examinations so rapidly that this alone would have marked him out for promotion. The earlier years of his Indian service were spent chiefly in the Province of Bengal, mainly in the Darjeeling Division; but varied by several years from 1890 as an Instructor in the Indian Forest School at Dehra Dun, as a result of which experience he wrote in three volumes 'A Manual of Forest Engineering for India'. When the book went out of print, he unfortunately was unable to find the time for the preparation of a new edition. In 1901 he was selected for the important charge of the Andaman Forest Circle; and he greatly increased the out-turn of valuable timber from the Andaman Islands by his energy and

enthusiasm. His work brought him into touch with the shy and suspicious aboriginal tribes : and on one occasion he was called on to accompany a small punitive expedition against certain marauders, whose camp was rushed at night when the police officer was killed by a spear at his side. He brought the party back to safety. After leave in 1906 he was promoted to be Conservator of Forests, Berar, in the Central Provinces. During his period of duty there he conducted experimental work on the use of temporary agricultural crops for nursing back into existence forest that had been destroyed. In 1910 he was transferred to the Pegu Circle of Burma, and in 1913 was selected for the important post of Chief Conservator of Forests in that Province. He held this post until his retirement in 1919, with a Companionship of the Indian Empire, very fully earned by long and meritorious service.

He was a most generous man and always willing to put his knowledge at the service of another or to put his own occupation on one side to help a friend. His active mind found interests extending from every corner of his profession—from the trees, their exploitation and their uses, to all manner of jungle produce, to the animals of the jungle, and to the jungle tribes. He made the most diverse collections, which, now, have been given to various museums ; his greatest interest outside forestry was in botany, and he did some research into the aconites of the Darjeeling Himalaya : but his duties left him little time for such work, which, moreover, was not officially encouraged.

After retirement from Indian service he visited East Africa and climbed in the mountains of Kenya and Kilimanjaro ; and then settled in England, first at Etchingham in Sussex, and later at Woking in Surrey, where he died after a short illness on 18 November 1937. His garden held growing plants which he had raised from seed collected in the equatorial mountains of Africa.

LEONARD ROGERS.

LIONEL WALTER, eldest of the three children of the first BARON ROTHSCHILD of Tring, was born in London on 8 February 1868. As a child, being considered too delicate to be sent to school, his education was carried on entirely at home under governess and tutor. Later, with the object of widening his interests and to improve his knowledge of the German language, he went to the University of Bonn, where he remained for two terms. On his return he went up to Magdalene College, Cambridge, for about two years. His interest in natural history was inherited, his father having been a keen botanist and a great lover of birds, encouraging his children to be the same. Walter commenced collecting

at the age of seven, and never lost interest in the subject. While at Cambridge he met Professor Alfred Newton and others who sympathized with and encouraged his keen interest in zoology and in intelligent collecting of zoological material, with the result that his collections increased to an extent necessitating their storage in rented rooms at Tring even while he was still at Magdalene. Dr. Albert Günther, then Keeper of Zoology at the British Museum, also influenced him in his study and line of work.

After leaving Cambridge Rothschild entered his father's Banking firm with the object of studying finance; and later became Liberal Unionist M.P. for the Aylesbury Division of Buckinghamshire, a constituency which he represented with success from 1899 to 1910, and which his father—as a member of the Liberal Party—had represented before him. Rothschild's real bent was, however, to natural science, and it is for his great accomplishments in that direction that his name will live for future generations. While engaged in the City and in the House of Commons he devoted the little spare time at his command to the study and furtherance of his collections. Already in 1889 the number of entomological specimens had become so large that a cottage had to be built for their accommodation and a larger building with it for the display of mounted specimens of all kinds. In August 1892 the Museum was opened to the public and a curator, Dr. Ernst Hartert, appointed. In 1893 Dr. K. Jordan became curator of Invertebrates, and from that time direct relations were established with collectors, scientists, and others in distant parts of the world with the object of securing specimens from outlying and little-known places. Then began Rothschild's first important work, the 'Avifauna of Laysan'—in three volumes (1893-1900),—the outcome of an exhaustive ornithological exploration of the Sandwich Islands Group, carried out by a sailor, Henry Palmer, under his direction and at his expense. His 'Revision of the Papilios of the Eastern Hemisphere exclusive of Africa', a work which had a marked influence on the methods of systematics in the Order to which they belong, was published in 1895; 'A Monograph of the Charaxes', 'Monograph of the Cassowaries', and 'a Revision of the American Papilios' are among the more important of his publications in collaboration with the Curators of Tring during the years 1897 to 1908. In 1910 he left the House of Commons, and two years earlier had retired from the City to devote himself more freely to his zoological work and the direction of Tring Museum. He undertook an interesting and successful collecting expedition in the North of Africa, but the fatigues necessarily connected with such expeditions were not suited to his con-

stitution and his last trip was made in 1914. From that time till the date of his death he occupied himself in trying to further the interests of zoology and in increasing the value and scientific usefulness of his Museum, which soon became the finest private institution of its kind in the world. From 1899 he had been a Trustee of the British Museum, and in 1911 was elected a Fellow of the Royal Society in recognition of his services to natural history.

Lord Rothschild was one of the greatest experts in the world on birds, and his collection at Tring unequalled anywhere. When in 1931 at the time of the general financial depression he suddenly found himself faced with a demand for payment of a very large sum of money, to his grief he was compelled to part with his beloved bird collection. It had taken over forty years to amass, and the blow was so great that he was unable to rise above it. Tring without the birds was no longer the same.

In 1935 a fall in the grounds of Tring Park injured his knee severely and he was compelled to remain in bed for five months. He recovered but partially and in the summer of 1937 grew much worse, dying in his sleep on 27 August.

Lord Rothschild's interest in the British Museum (Natural History) was almost as great as in Tring. By his will he left Tring Museum and its contents to the Trustees of the British Museum on condition that the Museum should be used for a zoological purpose and that the vast entomological collections should be kept intact. Lord Rothschild was strongly of opinion that sound views on the stability of zoological characters and geographical variation could only be formed on the basis of adequate material representing each species and subspecies. He took the strongest possible interest in systematics. His knowledge of species and subspecies of Lepidoptera, Mammals, Birds, and Reptiles was astounding, and his memory of characters and names seemed never to be at fault. A big man himself, he was particularly attracted by big specimens—giant tortoises, whales, and ratite birds were among his special favourites. He spared no expense in acquiring complete series of the finest zoological and entomological specimens of all kinds, and he built up one of the finest private libraries in the world dealing with his favourite studies. The presence of this library at Tring will enable the Museum there to become, under the Trustees of the British Museum, what it has always been under Lord Rothschild, a great centre of zoological research.

When one examines Tring Museum, its collections and its library—the long series of beautiful specimens representing nearly all the known species in many groups, and the complete collection of books, many of them of very great rarity—one

cannot repress a feeling of deep admiration not only for Lord Rothschild, but for his brother the late Hon. N. C. Rothschild, Dr. Hartert, and Dr. Jordan. It is difficult to believe that, even with riches to assist, four men could have produced so wonderful a temple of science within the space of fifty years. Great indeed is the power of enthusiasm. There is enough at Tring to keep several generations of research workers busy throughout their lives : and it will take many years to exhaust the possibilities of research at this moment available there.

M. A. C. HINTON.

ANNIE LORRAIN SMITH was born on 25 October 1854, at Half-morton, Dumfriesshire, where her father, the Rev. Walter Smith, was a minister of the Free Church of Scotland. She was one of a large and talented family, two of her brothers becoming professors of philosophy and one professor of pathology. Part of her education she received in Edinburgh : she also studied French at Orléans and German at Tübingen. For some years she was governess in private families. About 1888 she took up the study of Botany under Dr. D. H. Scott at the Royal College of Science, South Kensington, attending his classes and later working in his laboratory. Her earliest investigations were on seaweeds, carried on partly under Scott and partly in the Cryptogamic Department of the British Museum under George Murray, the results of which were published in the 'Phycological Memoirs', of which he was at that time editor. Her first practical connection with the Cryptogamic Department started when she was asked to remount the microscopic slides of the de Bary collection, and thus began an association with the Department which was to continue for the greater part of her life. Between 1892 and 1908 she arranged the exhibition stands of microfungi in the Botanical Gallery of the Museum. From 1899 to 1901 she held the post of Assistant to Dr. W. Carruthers (Keeper of the Botanical Department), who was then acting as Botanical Consultant to the Royal Agricultural Society : the work involved seed-testing and the examination of moulds often associated with seed-germination. Her account of these Fungi was published in the 'Journal of the Royal Microscopical Society' (1901, p. 613). She gradually acquired such a wide knowledge of Fungi that she was able to name collections sent to the Museum from tropical East Africa (Scott Elliot, J. W. Gregory, and W. E. Taylor), Angola (Welwitsch), and the West Indies (W. R. Elliott), and published notes on them.

But lichens were soon to absorb her special attention. By the death of the Rev. J. M. Crombie in 1906 his 'Monograph of British Lichens' was left unfinished, only volume 1 having been written. Miss Lorrain Smith undertook to complete the

second volume, which appeared in 1911; later she rewrote volume I (1918). This Monograph, published by the Trustees of the British Museum, is a standard work of great importance and gave her an authoritative position among lichenologists both at home and abroad. Meanwhile she arranged a series of British Lichens, for the use of students in the Botanical Gallery. She was engaged in preparing a second edition of the Monograph, one volume of which was completed (1926) when, four years ago, ill-health obliged her to desist. In 1921 she wrote a small 'Handbook', based on the Monograph, in the form of a Key to British Lichens, with numerous illustrations. In the same year was published her textbook on 'Lichens', one of the Cambridge Botanical Handbooks, a monumental work, dealing with the subject from many aspects, as bringing together a wealth of detailed information, admirably arranged and illustrated.

Her help in the Cryptogamic Department, always useful, was especially valued during the War when many of the staff were necessarily absent; she was appointed 'Acting Assistant', and was responsible for Lichens and Fungi, but she remained an 'unofficial worker' to the end.

Miss Lorrain Smith was one of the 'foundation members' of the British Mycological Society, which she joined in 1897. She was twice President, at Newcastle in 1907 and at Shrewsbury in 1917. She contributed many papers to its 'Transactions', chiefly on Microfungi and Lichens. Her knowledge, keenness, humour and geniality, and moreover her readiness to help others, especially the younger members, made her an ideal comrade during the annual meetings; these she attended whenever possible, up to the Haslemere meeting of 1932.

For more than thirty years she wrote Abstracts of recent papers on Fungi and Lichens for the 'Journal of the Royal Microscopical Society', a work much appreciated by fellow-students. She much enjoyed visits to the United States of America to see members of her family, and to Australia (1914) with the British Association party.

She was among the first women to be elected to the Fellowship of the Linnean Society (1904), and served on its Council from 1918 to 1921.

For many years she was a member of the South Eastern Union of Scientific Societies, and was President of the Botanical Section in 1922; she was an honorary member of the Quekett Microscopical Club and of the Essex Field Club; and served on the Council of the South London Botanical Institute and of the Gilbert White Fellowship. She was no sleeping member of these councils, but was alert to help by her wise judgment.

In 1934 the distinction of O.B.E. was conferred on her as a public recognition of her services.

Her life was enriched by wide interests and her convictions were strong. Her warm-hearted disposition, absolute integrity, and generous sympathy won her many friends. Her home, shared with an elder sister for fifty years, was a centre of gracious hospitality. When her sister died in 1933, Miss Annie felt her loss deeply. After a long illness, faced with courage and serenity, and cheered by the love of her friends, she passed away in her home in West Kensington on 7 September 1937, within a few weeks of attaining her eighty-third year.

GULIELMA LISTER.

Sir ALGERNON PHILLIP WITHIEL THOMAS, K.C.M.G., M.A., F.L.S., F.G.S.—Four or five decades ago the name of Thomas was familiar to zoologists, and especially to students, owing to his investigations into the Life History of the Liver fluke (*Fasciola hepatica*) undertaken in the first place on behalf of the Royal Agricultural Society and printed at length in the 'Quarterly Journal of Microscopical Science', vol. XXIII. During this research he established two important facts about the life-history, viz., that the intermediate host, at any rate in England, is the amphibious snail, *Limnaea truncatula*, and that the sheep become infected by eating a cyst formed by the cercaria on leaves of grass etc. He proved these facts by experiments. The search for the host was arduous, for there were at least a dozen species of mollusc with somewhat similar habitat, but by keeping these species in an aquarium in which embryo flukes were liberated he found that only the above-named species became infected. Further, he observed the liberation of the cercariae from the snail and the subsequent formation of a cyst by the glands on its surface. Normally this cyst is attached to leaves of grass etc. on the marshy ground on which the snail lives. It is by eating such grass that the sheep becomes infected with liver fluke. Hitherto it had been surmised that the sheep ate a snail which harboured a cercaria, but what species of snail was doubtful. This paper is illustrated by a series of excellent figures which appear in many text-books at the present day.

But from the 'eighties zoologists heard nothing further of Thomas and so far as zoological research was concerned he had disappeared, for in 1883, the year in which the above paper appeared, he was appointed Professor of Geology and 'Natural Science' in the newly founded University College at Auckland, where he was responsible for the teaching not only of zoology, but also of botany and geology up to honours standard in each subject. No wonder, then, that he produced so small an amount of original work.

Born in 1857, at Birkenhead : schooled in Manchester, he later went to Balliol College, Oxford. In 1879, after taking his B.A., he acted as biological demonstrator in the department under Professor Rolleston. He won a Burdett-Coutts scholarship, and it seems to have been then that he did his researches on the liver fluke.

Soon after his appointment to Auckland he undertook at the request of the Government to report on the parasites attacking sheep, which were mostly Nematodes.

In 1889 he reported upon the 'Parasitic Diseases affecting Rabbits'. He traced out the life-history of the Tapeworm, *Coenurus serialis* and its relation to the dog strobila : its effect on the health and death-rate of rabbits, discussing the importance of parasites in diminishing the rabbit pest.

This was the last of his zoological work, in spite of the abundant and tempting fauna, marine and terrestrial, by which he was surrounded ; but he produced three articles on geology and three on certain lowly plants.

The geological papers were published in the 'Transactions of the N.Z. Institute'. He found that 'The Rocks of the Taupo District' (1887) belong to the basic group of lavas such as were expelled during the Tarawera eruption, though, of course, not in connection with that : and that 'the rocks of the Kermadec Islands' are likewise volcanic.

In 'The Geology of the Tongariro and Taupo District' (1888) will be found an illustrated account of the chain of extinct volcanos, Ruapehu, Ngauruhoe, and Tongariro : of which the last has a hot lake in its crater from which considerable quantities of steam arise giving the impression of smoke, while the second is snow-clad, and also with a hot lake at the summit. He described the mineralogical constitution of the various rocks.

In 1888 at the request of the Minister for Mines he presented a masterly 'Report on the Eruption of Tarawera and Roto-mahana' which occurred on 6 June 1886 between 3 a.m. and 6 a.m. after at least five centuries of quiescence, for the Maoris had no tradition of such an event. He gives a vivid account of the eruption of this flat-topped mountain, the ashes from which were spread over an area of 6000 square miles, details of changes in the topography of the district and of the mineralogical nature of the ejections.

Then followed his botanical work. In his private garden at the Auckland suburb of Epsom, he specialized in the genus *Narcissus* and by cross-pollination of various strains produced some fine new varieties, the bulbs of which fetched good prices. In his laboratory he studied some of the endemic lower Cryptogams, for which he had to search arduously in the surrounding Bush country. On the Prothallium of

Phylloglossum (Proc. Roy. Soc. 1901), 'The Affinity of *Tmesipteris* with the Sphenophyllales' (Proc. Roy. Soc. 1902), and the third article appeared in the 'Annals of Botany' 1902, on 'An Alga-like Fern Prothallium'. These three articles are short and unillustrated. *Phylloglossum* is a genus with a single species confined to New Zealand and Australia, it is 'a permanently embryonic Lycopod' which lives symbiotically with a fungus, the presence of which in the soil is necessary for the germination of the spore. Hence the difficulty of finding it. Thomas regards its simplicity as primitive. The second article is concerned with the homology of the 'fertile structure', and with the divergent views of Bower and of Scott; from its anatomy and the varying conditions of the sporangiophore and the sporangium in *Tmesipteris* he believed that it and *Psilotum* are more closely allied than was supposed to the extinct Sphenophyllales. The subject has received more detailed attention in recent years from Dr. John Holloway, of Dunedin. The third paper deals with the primitive New Zealand fern *Schizaea*: Thomas compared the filamentous prothallus with the 'hypothetical algal ancestor of Mosses' as postulated by Goebel rather than with the protonema of existing Mosses.

Such is a summary of his scientific work.

He was elected to this Society in 1882. In 1937 his name appeared amongst the Coronation Honours: and he died on 28 December 1937 in his 81st year.

Apart from his professional duties, which he relinquished in 1914, he was actively interested in educational matters: was member of the Senate of the University of New Zealand for some years, and chairman of the Auckland Grammar School Board for 21 years up to the time of his death.

WM. B. BENHAM.

RICHARD FRANCIS TOWNDROW died at his house at Malvern Wells on the evening of Christmas Day 1937. He was born at Malvern Link on 29 October 1845, and had lived the whole of his long life in the neighbourhood of the home in which he was born.

On the death of his father he carried on the family business at Malvern Link, and continued to do so till his retirement twenty-six years ago, when he went to live at Malvern Wells. His study of botany was of necessity a recreation reserved for such leisure as could be spared from his business. As a field botanist he excelled, and the locality to which he devoted his research has benefited richly by the records of his work. A walking distance from his home included much delightful wild-flower country in both Worcestershire and Herefordshire, and he was familiar with every corner of the district and the

plant-life to be found there. His active nature and observant eyes missed no opportunity, and he knew how to absorb, and to dispense to others, the joy of his surroundings with almost boyish excitement. The Linnean Society recognized this and elected him an Associate in 1915.

Mr. Towndrow contributed several articles to the 'Malvern Advertiser' on the plants of the district. The first of these was printed in 1892. In this paper Mr. Towndrow speaks of his 'sixteen years' botanical search'. Earlier than this a series of papers had appeared on 'Butterflies and Moths' of the neighbourhood.

In the 'Botany of Worcestershire' (Amphlett and Rea, published in 1909) and also in the Appendix by Mr. Carleton Rea, concluded in 1931, Mr. Towndrow's name appears frequently, especially with reference to plants of the Malvern area. The discovery of *Sagina Reuteri* was recorded by Mr. Towndrow in the 'Journal of Botany' (1897, p. 409). The record of the discovery of *Rosa sempervirens* is given in the report of the 'Botanical Exchange Club for 1885-6'. Mr. Towndrow named this rose *Rosa Melvini* in honour of the friend who first drew his attention to it. An off-shoot from the original plant is now flourishing in the garden of the house in which he died. Mr. Towndrow states in one of his papers that a full account of this rose is given in the supplement to the third edition of 'English Botany', pp. 162-3. His account of his discovery of *Gagea fascicularis* in Worcestershire is recorded in the 'Journal of Botany' for June 1900.

A man of fine character; no one could be with him long without realizing something of the greatness hidden under his modest exterior.

His appearance was striking and unusual; his tall, slim figure and the dark, penetrating eyes gave the impression of energy and inspiration.

He wrote much poetry, but published little.

In a life many times clouded by sorrow and sadness he faced up with courage to meet each ordeal as it came, and to the end he maintained a serene and reverent outlook on life.

BEATRICE STUART.

EDWARD PHILLIPS TURNER (1865-1937) was born in 1865 at Havant, England. His father was Dr. Charles Turner (married Irene, daughter of Col. Pirie). He came to New Zealand with his parents in 1870. Later he went to Tasmania, where he received his education at the Hutchins School and by private tuition. At the age of sixteen he went to sea for a year. In 1882 he was studying in England. He then returned to Tasmania, and after an experience in farming came to New Zealand in 1884. He took up surveying, passing his exami-

nations for that profession in 1887. He surveyed in different parts of New Zealand and New South Wales. In 1891 he accepted a Government appointment to carry out surveys in the silver fields on the west coast of Tasmania. After a visit to England he returned to New Zealand in 1894 and joined the Government Survey Department at Auckland.

In 1907 Turner was appointed to the Labour Department at Wellington as Inspector of Scenic Reserves for the Dominion. In 1913 he was appointed Secretary to the Royal Commission on Forestry. The following year he was a member of the Royal Commission on the reservation of scenery along the Wanganui River. In 1918 he was placed in charge of the newly created forest branch of the Lands Department. In 1920 the department was again reorganized as the State Forest Service with Mr. L. M. Ellis as Director and Turner as Director of Forestry in charge of the administrative side. Ellis resigned in 1928 and Turner remained in charge of the service under the title of Director of Forestry until his retirement in 1931. Thereon he retired to Hamilton, where he continued his interest in forestry matters. He died on 20 May 1937 at Hamilton.

Turner took a great interest in the native life, more especially in the plants and birds of New Zealand. He collected specimens of plants, which he usually passed on to Mr. Cheeseman or Dr. Cockayne. Among his important discoveries was a new species of *Pittosporum* which Dr. Cheeseman described under the name of *Pittosporum Turneri*. Turner's exploratory work in botany was carried out mainly in the thermal region of the North Island. He ascended Mount Tarawera (scene of a violent eruption in 1886) in 1900, and again in 1927. As a result he contributed an account of the re-establishment of the vegetation of the higher Waimarino district, a locality west of, but adjacent to, the National Park. As a botanist, however, Turner is best known as junior author to Dr. Cockayne of a handbook entitled 'The Trees of New Zealand', published by the State Forest Service in 1928. This is a most useful guide to the Dominion's principal trees. In addition to these botanical contributions, he published a number of reports on forestry matters.

He was a Fellow of the Royal Geographical Society and a member of several other Societies whose activities were concerned in forestry, surveying, and botany.

Mr. Turner was of a most kindly disposition. No service that would assist his fellow-workers was too much trouble for him. His interest in the forests of New Zealand never waned, and up to his death we find him freely giving advice obtained during a lifetime devoted to the forest in all capacities from surveyor to administrator.

W. R. B. OLIVER.

JOHN AUGUSTUS VOELCKER, who died on 6 November 1938 at 83 years of age, was almost the last representative of the group of agricultural chemists which dominated the study of agricultural science during the last half of the 19th century. He was, so to speak, born into the middle of this group, for his father, Dr. Augustus Voelcker, was one of its most distinguished members in England, and exercised an almost unparalleled influence on the development of agricultural science between 1865 and his death in 1884. The subject of this notice was his eldest son ; and he was trained to succeed his father. He studied science at University College, London, then at Giessen, and finally at Cambridge, and then joined the laboratory which his father had established in London as a consulting agricultural chemist. This laboratory was unique at the time, and the methods used there, to which Dr. J. A. Voelcker adhered during almost all his life, have remained the basis on which the examination of agricultural materials is even now conducted all over the world.

On the death of his father in 1884, the subject of this notice was unexpectedly called upon to succeed the former both in his consulting practice and in the large number of public positions which he held. He rose to the occasion and was for many years the principal and almost undisputed authority on questions of the application of chemistry to agriculture. When I first knew him a few years later he was consulted from every part of the world, and his opinion, and the results of his analyses, were accepted as authoritative not only in England or in the British Empire, but in many other countries as well.

During his life he held a large number of public positions, the chief of these was, of course, that of consulting chemist to the Royal Agricultural Society ; and this position he retained until his death. His annual reports in this connection, of which the series is almost unbroken, and which are almost entirely based on work actually done in his laboratory, will be found a unique record of the changes which have taken place in the character of the feeding stuffs and fertilizers which are used in England. His services towards the purification of such materials have been very great and his investigations had a great deal to do with the passing of the Fertilizers and Feeding stuffs Acts in later years. Voelcker was also chemist to the Royal Horticultural Society and to other agricultural societies, and he held a number of positions as agricultural analyst under the Ministry of Agriculture. He was also for some time President of the Society of Public Analysts.

Voelcker became Director of the Woburn Experimental Station in 1884, soon after its establishment, and he remained in this position until September 1936. The experiments

which have been carried on at this Station formed one of the chief interests of his life, and they owe almost everything to the zeal and energy which he put into them. The problems which interested him most were those concerned with the reactions between various fertilizers and the soil, with the maintenance of the fertility of land by green manure or otherwise, and with the residual value of manures. The question of the residual value of manures was, in fact, that for which the Woburn Station had been founded in 1876. Almost all the work which he did at Woburn was described in the 'Journal of the Royal Agricultural Society', and the general results obtained during the first fifty years of the Station have been described in a book published by himself and Sir John Russell in 1936. It was a source of great satisfaction to him that he was able to co-operate in bringing out this monument of what he regarded to a large extent as his life work.

In 1889 Voelcker was invited by the Government of India to go to that country and report on the scientific improvement of Indian agriculture. His visit there in the years 1889-90 was a great success and his report has been the basis for most of the scientific work which has since been done in connection with agriculture in India. It was, in fact, found so valuable by the Royal Commission on Indian Agriculture in 1926 that he was decorated as C.I.E. on this account thirty-five years after the report was originally made.

Voelcker had a special bent for applying scientific results to practical problems, especially agricultural problems. He had, in fact, an almost uncanny knack of extracting, from comparatively simple experiments, conclusions which would stand the test of practice, and hence he was in great demand as adviser in agricultural difficulties. His interest in agriculture was profound, and nothing pleased him more than to spend time on a farm or to associate with those who were responsible for managing agricultural land. He was, in fact, President of the Farmers' Club in 1908.

Apart from his scientific activities Voelcker was a man of very wide interests. He was an athlete in his youth when he was a well-known cross-country runner, and a sportsman later in life. He never lost his zest for one or other and almost to the end of his life he could often be found on a Saturday afternoon attending the events of the London Athletic Club of which he was twice President. This illustrates the broad outlook on life which he possessed, and this, together with his sterling character and capacity for understanding other points of view than his own, secured for him a very large circle of friends. He retained his energy and his fresh points of view to the last and, despite his great age, his passing leaves a gap which will be very hard to fill.—HAROLD H. MANN.

Sir OSCAR EMANUEL WARBURG, O.B.E., died on 1 July 1937 at the age of 61.

Born in London on 6 February 1876, and educated at Trinity College, Cambridge, Sir Oscar was one of that numerous band of English business men and men of affairs who find their recreation in the study of natural history and the growing of plants, and who so master their chosen subject that they come to be looked to as authorities upon it. He collected in their native homes many, and, in the large garden of his house, Boidier, near the crest of Pebblecombe Hill, Headley, Surrey, cultivated and studied all species and hybrids known in the genus *Cistus*, and with the generosity of the true gardener shared his plants freely with those who desired to grow them. With his son, E. F. Warburg, he gathered a great collection of oaks from all over the world and planted all that stood the least chance of surviving in this country, and they together also planted all available forms of the British representatives of the genus *Sorbus*. He wrote an account of the genus *Cistus* in the 'Journal of the Royal Horticultural Society' (vol. LV, p. 1), and of the hybrids (in vol. LVI, p. 217), and Sir Oscar and his son dealt with the oaks in cultivation in the British Isles in the same Journal (vol. LVIII, p. 176). The carefully prepared specimens of all of these in his herbarium were a pleasure to examine and most helpful to study.

Sir Oscar took great interest in local government, and was Chairman of several Committees of the London County Council, of which he was a member for the North Hackney Division from 1920 to 1931 and an Alderman from 1931. He was Chairman of the London County Council 1925-26 and was knighted in 1926. During the European War he served as Captain in the R.G.A. (Special Reserve) and in the Intelligence Corps.

F. J. CHITTENDEN.

CHARLES WATERFALL died at Chester on 26 January 1938 at the age of eighty-seven. For sixty-two years he had been greatly interested in British botany; had a good herbarium of British plants collected in different parts of the British Isles; and in 1936 was awarded the Kingsley Medal by the Chester Society of Natural Science, of which he was an active member. He was elected a Fellow of the Linnean Society on 1 June 1911.—S. SAVAGE.

ALEXANDER ZAHLBRUCKNER (1860-1938), who died on 8 May at Vienna, had been a foreign member of the Linnean Society since 1925. His death was felt by the lichenological world to be one of the most serious losses it has sustained.

He was born at St. Georgen, and from the local school passed on to the University of Vienna, where he obtained the degree of Doctor of Philosophy at the age of 23.

Like so many other cryptogamic botanists his earlier work was on flowering plants, but during the last fifty years most of his work has been connected with lichens. Numerous papers on these puzzling plants were written whilst he was in the botanical department of the Vienna State Museum of Natural History, of which he became the Director in 1918. Before he retired in 1922 he had begun the monumental work which has earned for him the great respect and gratitude of lichenologists all over the world. This was the 'Catalogus Lichenum Universalis', in which the names of genera, species, varieties, and forms of lichens were given with reference to the author, date, and method of publication and synonymy. The first volume was published in 1921. The labour of sorting out the welter of lichenological data seemed almost an impossible task, but the chaos was gradually reduced to order, and it is a source of gratification that the ninth and last volume was completed four years ago. Perhaps the other most important work which Zahlbruckner accomplished was the great taxonomical advance which he gave when he framed the classification of lichens in Engler and Prantl's 'Die Natürlichen Pflanzenfamilien' (1898-1907), which, in general, has superseded all previous methods. His intimate knowledge of lichens from all over the world, as revealed in his numerous other papers, enabled him to grasp in a comprehensive manner their relationships to one another, and Zahlbruckner's system was followed to a great extent in the 'Monograph of British Lichens' issued from the British Museum by Miss A. Lorrain Smith from 1911 to 1926. The reformer is not always welcomed, but Zahlbruckner's views were never given in such an unkindly or dogmatic manner as to cause any personal rancour. He was always ready to welcome and acknowledge any views which tended towards a better elucidation of the problems connected with the group of plants favoured by his attention. A grand old master of his subject is gone and a great blank is left in the ranks of lichenology.—W. WATSON.

BENEFACTIONS

LIST in accordance with *Bye-Laws, Chap. XVII. Sect. 1, of all Donations of the amount or value of Twenty pounds and upwards, received during the past Twenty years.*

1919

Dr. B. Daydon Jackson : MS. index to Linnean Society's Journal, Botany, vols. xxi-xl (1884-1912) and the botanic entries in the 'Proceedings' for the same period.

1920

The Royal Society : Third contribution towards the printing of Mr. C. F. M. Swynnerton's paper as above, £50.

The High Commissioner for the Union of South Africa, for the printing of Dr. J. D. F. Gilchrist's paper on *Jasus Lalandii*, Part II, £60.

1921

The Percy Sladen Memorial Fund : Additional Grant in aid of publication of 'Transactions', 2nd ser., Zoology, vol. xvii, part 4, £72 10s.

The same : Grant in aid of publication of four papers on the Houtman Abrolhos Islands, £100.

The Royal Society : Donation in aid of papers by Mr. N. E. Brown and Mr. S. L. Moore, £90.

Dr. W. Rushton Parker : Donation of a large series of portraits of Naturalists and Persons after whom Genera have been named, and work on rearrangement and annotation of the entire collection.

Prof. C. S. Sargent, F.M.L.S. : Eight volumes issued by the Arnold Arboretum including 'The Bradley Bibliography'.

Dr. B. Daydon Jackson : MS. Catalogue of each sheet in the Linnaean Herbarium ; bound in two volumes folio.

1922

The late Sir Joseph Hooker: Donation of his Medals and Decorations. (Reversion to Linnean Society on Lady Hooker's decease.)

Anonymous donation in aid of publication of the late Dr. E. A. Newell Arber's paper, entitled 'Critical Studies of Coal-Measure Plant-impressions', £60.

The Percy Sladen Memorial Fund: Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xviii, pt. 1.

1923

Dr. W. Rushton Parker: (1) Donation of Oxford New English Dictionary; vols. i-x, 1888-1928, and Supplement, 1933, 4to. (2) Encyclopaedia Britannica: ed. XI, Cambridge, 1920-2. 32 vols. 4to.

E. Heron-Allen, Esq., F.R.S.: Contribution of £25 towards the cost of paper on the Foraminifera of Lord Howe Island.

1924

The Percy Sladen Memorial Fund: Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xviii, pt. 2.

1925

Mr. Reginald Cory: New Presidential Chair, emblazoned with the Arms of the Society.

1926

Subscription portrait of Dr. B. D. Jackson, R.N.O.

Mr. A. D. Michael: A large number of Books and Pamphlets from his Library.

The late Mr. A. O. Walker: £200 free of Legacy Duty.

An Anonymous Donor: £100 to establish a Fellowship in memory of the late Prof. E. A. Minchin, F.R.S., Sec.L.S.

The Royal Society: Donation in aid of publication of Mr. G. P. Farran's paper on Biscayan Plankton.—Part 14. The Copepoda, £60.

The late Mr. Frank Morey: £100 free of Legacy Duty.

The late Mr. George Lewis: Books and pamphlets on Entomological subjects.

Capt. E. G. Spencer-Churchill: A copy of a collotype reproduction of 'The herbal of Apuleius Barbarus . . . (MS. Bodley 130) '.

The Percy Sladen Memorial Fund: Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xix, pt. 1.

1927

The late Mrs. Mary Anne Stebbing: £100 less Legacy Duty.

1928

Carnegie United Kingdom Trust: £666 13s. 4d. for purchase of books.

The Royal Society: £160 (£85 in aid of the publication of Dr. G. Enderlein's paper on 'Die Copeognathen der Seychellen', £75 in aid of Mr. C. V. B. Marquand's paper on 'The Botanical Collections made by Capt. F. Kingdon Ward in the Eastern Himalaya and Tibet in 1924-5').

1929

Carnegie United Kingdom Trust: £666 13s. 4d. for purchase of books.

The Percy Sladen Memorial Fund: £100 in aid of the publication of papers on the Fauna of the Paraguayan Chaco.

Carnegie Trust for the Universities of Scotland: £28 in aid of the publication of papers on the Fauna of the Paraguayan Chaco.

1930

Carnegie United Kingdom Trust: £666 13s. 4d. for purchase of books.

An Anonymous Donor: £23 towards the purchase of an Epidiascope.

The Royal Society: £100 in aid of the publication of Mr. H. W. Pugsley's paper, 'A revision of the British *Euphrasiae*' and Dr. T. A. Sprague's paper, 'The Herbal of Leonhart Fuchs'.

Mrs. B. Daydon Jackson (the late): valuable reversion under her Will after three life-tenants shall have died.

Mr. B. B. Woodward (the late) and Mr. A. S. Kennard: a portion of Mr. Woodward's scientific library and reversion of the remainder.

1931

- Miss E. C. Hatchett Jackson: Bust of Charles Hatchett, F.L.S., by Chantrey.
- Major Vivian Seymer: Volumes from the Library of Henry Seymer.
- Exors. of the late Dr. E. J. Bles: Donation in aid of colour collotype plates to illustrate Dr. Karl Peter's paper on *Xenopus laevis*, £100.
- Dr. Francis Pierrepont Barnard: Bequest of Sir James E. Smith's seal, his collection of seal impressions, and some portraits.
- The Percy Sladen Memorial Fund: Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xix, pt. 2.

1932

- Mr. Francis Druce: Donation towards the cost of new books, £50.
- The Royal Society: Donation in aid of the publication of papers resulting from Dr. Worthington's Expedition to the East African Lakes, £75.
- Subscription portrait of the late Professor Julius von Sachs, F.M.L.S.
- Cambridge Expedition to the East African Lakes, 1930-31 (Dr. E. B. Worthington, leader).—Unexpended balance of expedition funds, for the publication of the scientific results, £175.
- Carnegie Institution of Washington: Donation of a considerable number of its publications.

1933

- The Royal Society: Donation in aid of the publication of Dr. H. Boschma's paper, 'The Rhizocephala in the collection of the British Museum', £60.
- The Percy Sladen Memorial Fund: Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xix, pt. 3.

1934

- Mr. Francis Druce: Certain legal expenses connected with the Society's interest in the Will of the late Mrs. Jane Jackson, £33 14s.

- Mr. Warren R. Dawson, F.R.S.E. : Compilation of ' Catalogue of the Manuscripts in the Library of the Linnean Society of London.—Part 1. The Smith Papers'; and cost of binding the additional series of correspondence, etc.
- The Royal Society : Donation in aid of the publication of Dr. G. S. Carter's paper, ' The fresh waters of the rain-forest areas of British Guiana ', and Mr. H. N. Dixon's paper, ' A contribution to the Moss flora of Borneo ', £85.
- The Misses Phipps Tiarks : Copy of portrait of N. B. Ward, F.R.S., F.L.S., by an unknown artist ; engraving after Knight's portrait ; drawing of Ward's conservatory ; and his ' Pitt Club ' medal.

1935

- The Royal Society : Donation in aid of the publication of Mr. W. T. Stearn's paper, ' *Epimedium* and *Vancouveria*, a monograph ', and Dr. F. K. Sparrow's paper, ' A contribution to our knowledge of the Aquatic Phycomycetes of Great Britain ', £150.

1936

- The Trustees of the Will of Herbert Spencer, deceased : £1241 in payment of bequest.
- The Royal Society : Donation in aid of the publication of Mr. W. R. Philipson's paper, ' A revision of the British species of the genus *Agrostis* Linn.' and Dr. E. Fischer-Piette's paper, ' Études sur la biogéographie inter-cotidale des deux rives de la Manche ', £180.
- The late Lord Wakehurst of Ardingly : £100 free of Legacy Duty.

1937

- Prof. F. E. Weiss, F.R.S. : Zeitschrift für induktive Abstammungs- und Vererbungslehre, Bande 67-73, 1934-37.
- The Royal Society : Donation in aid of the publication of Dr. T. A. and Miss Sprague's paper, ' The herbal of Valerius Cordus ', £20.

1938

- The late Mr. E. T. Browne : A portion of his scientific library.
- Mr. Francis Druce : The expenses of the Society's 150th Anniversary Celebrations, £197 10s.

The Royal Society: Donation in aid of the publication of Dr. M. Carleton's paper, 'The biology of *Pontania proxima* Lep., the Bean Gall Sawfly of Willows', and Mr. I. Mackenzie Lamb's paper, 'A review of the genus *Neuropogon* (Nees et Flot.) Nyl., with special reference to the Antarctic species', £200.

TREASURER'S ACCOUNTS FOR THE

(Presented at the Anniversary

Receipts and Payments of the Linnean Society

General

	RECEIPTS	£	s.	d.	£	s.	d.
To Balance at 1 May 1937		1915	2	3			
„ Cash in hand		10	16	4			
					1925	18	7
„ Admission Fees					44	0	0
„ Arrears of Annual Contributions		36	0	0			
„ Annual Contributions for year		2434	0	0			
Do. in advance		117	0	0			
					2587	0	0
„ Interest on Investments (including Income Tax recovered)					315	2	0
Do. Deposit					7	1	7
Do. Post Office Savings Bank Account					24	3	4
„ Sales of Publications :—							
Transactions		20	3	11			
Journals		193	13	3			
Proceedings		17	12	0			
Library Catalogue		1	18	9			
Catalogue of Manuscripts		3	17	6			
					237	5	5
„ Advertisements :—Proceedings					13	17	4
„ Donations in aid of Publications					20	0	0
„ Donations for General Purposes					1	0	0
„ Miscellaneous Receipts					31	16	10

£5207 5 1

Library

	RECEIPTS	£	s.	d.
To Balance 1 May 1937		67	17	8
„ Interest on Investments (including Income Tax recovered)		49	9	1
„ Transferred from General Account		450	0	0
Do. Do. Herbert Spencer Bequest		49	13	6
Do. Do. Lord Wakehurst Bequest		100	0	0

£717 0 3

Fellows Postal

	£	s.	d.
To Balance at 1 May 1937	52	6	6
„ Deposits during year	18	0	

£53 4 6

YEAR ENDED 30 APRIL 1938.

Meeting, 24 May 1938.)

from 1 May 1937 to 30 April 1938.

Account

	PAYMENTS	£	s.	d.	£	s.	d.
By Coal, Electric Current, and Gas.....		92	18	9			
„ Furniture.....		7	2	8			
„ Repairs: Sundry		9	6	4			
„ Taxes and Insurance		58	16	5			
„ Miscellaneous Printing and Stationery.....		152	14	0			
„ Petty Expenses (including Tea and Postage)		188	15	4			
„ Publications:—							
Printing		919	17	0			
Illustrations.....		165	4	4			
Distribution.....		92	9	7			
					1177	10	11
„ Salaries and Wages, etc.					1179	6	8
„ Coronation Decorations					30	12	3
„ Transferred to Library Account					450	0	0
„ Zoological Record: Donation for 1937 volume					15	0	0
„ International Commission of Zoological Nomenclature—Donation					10	0	0
„ Purchase of £99 0s. 10d. 3½ per cent. Conversion Stock (Staff Pension Fund)					100	0	0
„ Linnean Medal					15	15	0
„ Herbert Spencer Bequest:—							
Renovations to Meeting Room, etc..	311	10	2				
Transferred to Library Account.....	49	13	6				
					361	3	8
„ Lord Wakehurst Bequest: transferred to Library Account					100	0	0
„ Balance at 30 April 1938:—							
Current Account at Bank.....	151	4	3				
Deposit Account Post Office Savings Bank	520	9	9				
Deposit Account Post Office Savings Bank (Herbert Spencer Bequest)..	579	10	3				
Cash in hand	6	18	10				
					1258	3	1
					£5207	5	1

Account

	PAYMENTS	£	s.	d.
By Books		19	16	11
Do. Herbert Spencer Bequest		29	5	10
„ Periodicals.....		336	11	7
„ Do. Herbert Spencer Bequest		3	6	8
„ Binding		145	3	9
„ Do. Herbert Spencer Bequest		17	1	0
„ Purchase of £103 12s. 5d. Surrey County 3 per cent. Stock (Lord Wakehurst Bequest).....		100	0	0
„ Balance at 30 April 1938		65	14	6
		£717	0	3

Account

	£	s.	d.
By Postage during year.....	1	6	6
„ Balance at 30 April 1938	51	18	0
	£53	4	6

To Balance at 1 May 1937 :—		£	s.	d.
Westwood Fund	£28	12	11	
Trail Award Fund	25	1	8	
Crisp Award Fund	76	14	7	
Hooker Lecture Fund	57	17	1	
Goodenough Fund	2	8	11	
Minchin Fellowship Fund	8	6	2	
		199	1	4
" Interest on Investments (including Income Tax recovered) :—				
Westwood Fund	£11	12	6	
Trail Award Fund	3	10	0	
Crisp Award Fund	7	14	0	
Hooker Lecture Fund	22	12	6	
Goodenough Fund	9	4	4	
Minchin Fellowship Fund	4	18	10	
Staff Pension Fund	43	2	10	
		102	15	0
By Goodenough Fund :—				
Transferred to Annual Contributions				£
Trail Award Fund : cost of Medal and Award ..				10
Minchin Fellowship Fund :—				16
Transferred to Annual Contributions				12
Westwood Fund : cost of Illustrations				4
Crisp Award Fund—purchase of £109 11s. 1d. 2½ per cent. Consolidated Stock				8
Staff Pension Fund :—				11
Purchase of £42 19s. 4d. 3½ per cent. Conversion Stock				82
Balance at 30 April 1938 :—				11
Westwood Fund	£31	17	5	
Trail Award Fund	11	19	2	
Crisp Award Fund	1	17	6	
Hooker Lecture Fund	80	9	7	
Goodenough Fund	1	3	3	
Minchin Fellowship Fund	9	5	0	
		136	11	11
		£301	16	4

Westwood Fund	£28 12 11
Trail Award Fund.....	25 1 8
Crisp Award Fund	76 14 7
Hooker Lecture Fund	57 17 1
Goodenough Fund	2 8 11
Minchin Fellowship Fund	6 6 2

Westwood Fund	£11 12 6
Trail Award Fund	3 10 0
Crisp Award Fund	7 14 0
Hooker Lecture Fund	22 12 6
Goodenough Fund	9 4 4
Minchin Fellowship Fund	4 18 10
Pension Fund	4 2 10

102 15 0

£301 18 4

136 11 11

£301 16 4

30 April 1938.

General Account

	£	s.	d.
Metropolitan 3 per cent. Stock 1941	@ 102½	1027	10 0
India 3 per cent. Stock	@ 80	960	0 0
Eastern Bengal Railway 4 per cent. Irredeemable Debenture Stock	@ 99½	995	0 0
Great Western Railway 4 per cent. Debenture Stock	@ 110	1100	0 0
London Midland & Scottish Railway 4 per cent. Preference Stock	@ 76½	238	1 4
4½ per cent. Conversion Stock 1940-44	@ 106½	3501	19 2
3½ per cent. War Stock	@ 101½	280	19 7
	£8103	10	1

Library Account

	£	s.	d.
Forth Bridge Railway 4 per cent. Stock (Bentham Bequest)	@ 100½	452	5 0
4½ per cent. Conversion Stock 1940-44 (Walker and Morey Bequest)	@ 106½	212	10 0
East Indian Railway 3½ per cent. Debenture Stock (Tagart Bequest)	@ 87½	463	15 0
London County 5 per cent. Stock 1940-60 (Stebbing Bequest)	@ 105	92	18 2
Surrey County 3 per cent. Stock 1961-66 (Wakehurst Bequest)	@ 95½	98	14 0
	£1320	2	2

Separate Account

	£	s.	d.
Metropolitan Water Board 3 per cent. "B" Stock (Westwood Fund)	@ 89	206	14 0
Ditto	@ 89	594	5 3
Ditto	@ 89	145	11 6
New South Wales 3½ per cent. Stock, 1930-50 (Trail Award Fund)	@ 97	97	0 0
2½ per cent. Consolidated Stock (Crisp Award Fund)	@ 74½	305	2 5
India 3½ per cent. Stock 1931 (Westwood Fund)	@ 93	120	9 2
Ditto	@ 93	57	11 5
Ditto	@ 93	115	2 7
London County 5 per cent. Stock 1940-60 (Minchin Fellowship Fund)	@ 105	105	0 0
3½ per cent. Conversion Stock (Staff Pension Fund)	@ 102	1369	5 7
(£21 11s. 2d. Ditto, to be transferred on 1 May 1938.)			
	£3116	1	11

FRANCIS DRUCE, *Treasurer.*

We have (in conjunction with the Professional Auditor, who certifies as to all details) audited the Accounts of the Society for the year ended 30 April 1938, and found them correct. We have verified the Investments and Bank Balances.

Dated this 19 May 1938.

Auditors.
 J. RAMSBOTTOM,
 I. HENRY BURKILL,
 MARTIN A. C. HINTON,
 D. J. SCOURFIELD,
 B. BARNES,
 R. H. BURNE,
 T. A. SPRAGUE,

W. B. KEEN, *Chartered Accountant,*
 23 Queen Victoria Street,
 London, E.C. 4.

ADDITIONS AND DONATIONS

TO THE

LIBRARY

1937-38

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

-
- Adamson, R. S.** Notes on the vegetation of the Kamiesberg. (Bot. Surv. South Africa, Mem. 18, 1938, pp. 25.) 8vo.
[DEPT. AGRIC., S. AFRICA.]
- Afalo, F. G.** The sea-fishing industry of England and Wales. Pp. xx+386. 8vo. London, 1904. [EXORS. E. T. BROWNE.]
- Aitken, R. D.** *See Bews, J. W.*
- Allee, W. C.** *See Hesse, R.*
- Annuario della Pontifica Accademia delle Scienze.** Vol. 1. Pp. lxxxix+809+38. 8vo. Città del Vaticano, 1937. [FRATER AGOSTINO GEMELLI.]
- Atkinson, J. C.** British Birds' Eggs and Nests. Pp. viii+182. 8vo. London, 1862. [EXORS. E. T. BROWNE.]
- Aymar, G. C.** Bird flight. Pp. xii+234. 4to. London, 1936. [EXORS. E. T. BROWNE.]
- Baker, E. C. Stuart.** The Indian Ducks and their allies. Pp. xi+292. 8vo. London, 1908. [N. B. KINNEAR.]
- Indian Pigeons and Doves. Pp. xv+260. 8vo. London, 1913. [N. B. KINNEAR.]
- Balfour, F. M.** A Treatise on Comparative Embryology. Ed. 2. 2 vols. Pp. xi+591; xi+792. 8vo. London, 1885. [EXORS. E. T. BROWNE.]
- Barnes, B.** *See Gwynne-Vaughan, Dame Helen C. I.*
- Barnes, J.** *See Kearton, C.*
- Bateson, W.** Materials for the study of Variation, treated with especial regard to Discontinuity in the Origin of Species. Pp. xvi+598. 8vo. London, 1894. [EXORS. E. T. BROWNE.]
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